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The Canadian Entomologist

Vol. XCI Ottawa, Canada, September 1959 No. 9

Reproduction of the Pine Needle Scale, *Phenacaspis pinifoliae* (Fitch), (Homoptera : Diaspididae)[1]

By C. E. Brown[2]

Introduction

Investigations have shown that several types of reproduction commonly occur in the Coccoidea. Some species reproduce in the usual sexual manner, some parthenogenetically, some by either of these two methods depending upon whether or not fertilization takes place; others reproduce hermaphroditically. The type of reproduction is not confined to any particular group but is found throughout the superfamily.

Schrader (1929), by cytological examination, showed that *Aspidiotus hederae* (Vall.) reproduced by typical diploid parthenogenesis. Because of reports of male *A. hederae* by other workers he concluded that there were two races within the species, one with obligatory, and the other with facultative, parthenogenetic reproduction.

Hughes-Schrader (1930) found that the iceryine coccids reproduced in several ways. One species, *Icerya purchasi* Mask., reproduced hermaphroditically with occasional males being produced. These males mated with the females, but it was not known if their sperm was functional. The males of this species were haploid, the females diploid; the males were produced parthenogenetically. *Icerya montserratensis* Riley and Howard, and *I. littoralis* Ckll. produced only males when not fertilized, and males and females in about equal numbers when fertilized. The high percentage of males produced by some fertilized females was thought to be due to insufficient sperm, or fertilization after some of the ova had begun haploid development.

Basinger (1934) found that the mealy bugs, *Pseudococcus gahani* Green, and *Phenacoccus gossypii* T. & Ckll. were unable to produce eggs unless fertilized; the former species made an unsuccessful attempt to produce an egg sac, and the females of both species lived much longer than fertilized females.

James (1937) in trying to explain the abnormal sex-ratio of many species when a delay in fertilization occurred, proved that the resulting preponderance of males was not due to a non-disjunction of the x-chromosome when the female was of the homogametic type, as was formerly supposed. Working with *Pseudococcus citri* Risso, he found no parthenogenetic reproduction. A preponderance of males resulted when fertilization was delayed. James (1939) working with other species of scale, reported the following types of reproduction: (1) parthenogenesis with occasional males produced because of external stimuli, (2) functional hermaphroditism with or without males, (3) two races within a species, one with obligatory parthenogenesis producing only females, the other with dioecious sexual reproduction but with facultative parthenogenesis in the absence of males.

Stafford (1947) found that the olive scale, *Parlatoria oleae* (Colvee), was unable to reproduce parthenogenetically and that unfertilized females produced no eggs. They produced badly distorted scales and lived much longer than fertilized females.

[1]Contribution No. 560, Division of Forest Biology, Research Branch, Department of Agriculture, Ottawa, Canada; based in part on a thesis presented to the Faculty of the Graduate School of the University of Minnesota in partial fulfilment of the requirements for the degree of Master of Science.

[2]Forest Biology Laboratory, Calgary, Alberta.

Wigglesworth (1950), in discussing the effect of impregnation, stated that in many insects it was a necessary stimulation to oviposition. Some insects such as *Cimex* produced no eggs until after impregnation. In *Thermobia*, eggs were produced within the body of the female but impregnation was necessary before oviposition began. In many Lepidoptera and Diptera, unfertilized females lay about one third of their normal number of eggs.

The sex-ratio of insects has frequently been given as an indication of whether or not parthenogenetic reproduction takes place. It has been generally accepted that the ratio of males to females in the pine needle scale was one to one. Le Baron (1871) stated that "about equal numbers of males were found"; similar remarks were found in the writings of other authors. Unpublished reports of the Indian Head Forest Biology Laboratory (Peterson 1932-1950) indicate that the sexes were produced in approximately equal numbers. Cumming (1953) found ratios of approximately two males to three females on spruce, and one to one on pine. Few other data are available on the sex-ratio of this insect.

Materials and Methods

In order to determine whether or not fertilization was required, it was necessary to remove the males from the population before fertilization occurred. Five experiments were necessary before definite results were obtained. In the first experiment a small infested tree was placed in a rearing cabinet in the laboratory and removal of the males attempted. Although this experiment was not successful, the length of life of the females which did not lay eggs was considered important. The second, on white spruce, was prepared in 1950 at two locations in the town of Indian Head. The third and fourth, in 1951 on Scots pine, were located at the Forest Nursery Station, Indian Head, Sask. For these experiments, twigs two to three inches long were enclosed in finely woven nylon bags. The needles were removed from about three quarters of an inch of the twig at the proximal end to facilitate closing the bags. The male scales and the parent female scales were removed, leaving only the current year's virgin females on the sample. The twigs used as controls were prepared in the same manner except that the males and old females were not removed.

In 1957, the fifth experiment utilized small potted lodgepole pines, *Pinus contorta* Dougl. *latifolia* Engelm., placed under infested trees in the Crowsnest Pass, Alta. After the crawler stage was passed and the young nymphs were thoroughly established, the trees were removed to the Kananaskis Forest Experiment Station, where, as far as is known, no scale populations exist. The trees were left outdoors until the sexes could be distinguished, then were transferred indoors where the males and most of the needles were removed. The twigs selected for the samples were examined and only those needles with females on them were left on the twigs. The twigs were then enclosed in thin plastic (saran wrap) and were kept out of direct sunlight. The plastic was kept in place for approximately two weeks and did not seem to affect the growth of the scale or the functioning of the needles.

Results

Mating

Mating of the pine needle scale was observed under natural conditions. Soon after emergence the male (Fig. 1) began searching for the female, flying from twig to twig and running rapidly up and down the needles. Sometimes he ran over several females without appearing to notice them. Hughes-Schrader (1930) suggested that females which were fertilized were no longer attractive to the male. When a suitable female was located the male placed himself on top.

Fig. 1. Male of the pine needle scale (about 35X).

He had difficulty orientating himself and repeated attempts were necessary before copulation occurred. These females did not visibly respond to the approach of the male.

Reproduction

Five experiments were necessary before the type of reproduction was determined. Data on egg laying from the first experiment were discarded because male scales were found on the needles after some females had matured. Data on the length of time non-egg-laying females lived was retained because Stafford (1947) found that unfertilized females of the olive scale lived much longer than fertilized females and Cumming (1950) found that females of the pine needle scale died once oviposition is complete. Non-egg-laying females kept in the rearing cabinet lived much longer than those which had oviposited and were still alive after the nymphs of the egg-laying females had hatched and settled down. Many of these non-egg-laying females produced badly distorted scales similar to those described later.

When counts were made in 1950, it was assumed that unfertilized females were capable of producing young and an attempt was made to distinguish between the sex-ratios of the progeny of mated and unmated females. No definite sex-ratios or trends in sex-ratios could be established and the results were discarded.

Observations made while counting the above samples indicated that unfertilized females did not lay eggs, consequently the samples prepared in 1951 and 1952 were examined for evidence of oviposition rather than to differentiate between the progeny of mated and unmated females.

The average percentage of females which laid eggs under natural conditions at Indian Head, Sask., is shown in Table I (Peterson 1932-1950). The high percentage of females which laid eggs indicates that if fertilization is necessary, either the males fertilized only one female and were nearly always found in numbers which were equal to or exceeded those of the females, or that each male was capable of fertilizing more than one female. An average of the data for these years showed that only about six per cent of all the females did not lay eggs.

The results of the third and fourth experiments tended to confirm the opinion that fertilization is necessary for egg laying. Since more samples were prepared and more conclusive evidence was obtained in 1952, the figures for 1951 have been

TABLE I.

The number and percentage of females of the pine needle scale which laid eggs, Indian Head, Sask.

Year	Total number of females	Number of females which laid eggs	Percentage of females which laid eggs
1932	1271	1257	98.90
1934	56	51	91.07
1939	173	157	90.75
1940	1288	1185	92.00
1941	28333	28211	99.57
1942	727	700	96.29
1946	429	422	98.37
1950	7707	6706	87.01
1951	977	855	90.58
Total	40961	39544	96.54

placed in brackets. The percentage of females which laid eggs in the samples on which bags were placed to exclude the males was 2.5 (11.6) per cent while the percentage of females which laid eggs when the males had free access to the females was 94.9 (91.7) per cent. The average number of eggs laid per female when the samples were bagged was 0.66 (2.4) but when the males had free access to the females it was 40.4 (30.7). The average number of eggs for the 25 (11) out of 993 (95) bagged females which laid eggs was 26.2 (20.4) per female. Since only 36 or 3.3 per cent of the 1,088 females (all samples) laid eggs and since the bagged females laid an average of only 0.81 eggs it is evident that the attempt to exclude the males had a definite effect on egg production. Approximately one-third of the samples which were bagged to exclude males contained some females which laid eggs. These were believed to have been fertilized by males which entered or were left in the bags. The average number of eggs laid by these females was smaller than the average of the unbagged females due to the effects of bagging the twigs (Brown 1954).

Many of the females which did not lay eggs were alive and had produced a much distorted scale (Fig. 2), similar to those produced by unfertilized females of the olive scale (Stafford 1947). Fertilization of the pine needle scale usually takes place shortly after the scale begins to form but in some years may take place after a considerable proportion of the scale has been produced (Cumming 1950). The scales produced by the females which did not lay eggs were normal for one-quarter or more of their length (Fig. 2c) then became irregular, consisted of large lumps (Fig. 2d), or were irregularly twisted about the needle (Fig. 2 e-g). Many of the females had produced a longer than normal scale then pushed themselves backward until in many instances the abdomen protruded from the posterior end of the scale. Others produced irregular lobes of scale which covered only about one half of the body.

In the 1957 experiment in which the author was confident that males had been excluded, conclusive evidence that fertilization is necessary was obtained. In the eight samples containing 104 females (Table II) not one female produced an egg when the males were removed.

The females in these samples produced distorted scales similar to those recorded in the previous experiments (Fig. 2). In the check sample, where males had free access to the females, 76.9 per cent of the females laid eggs. Observations in the Crowsnest Pass indicated that a lower percentage of the females feeding

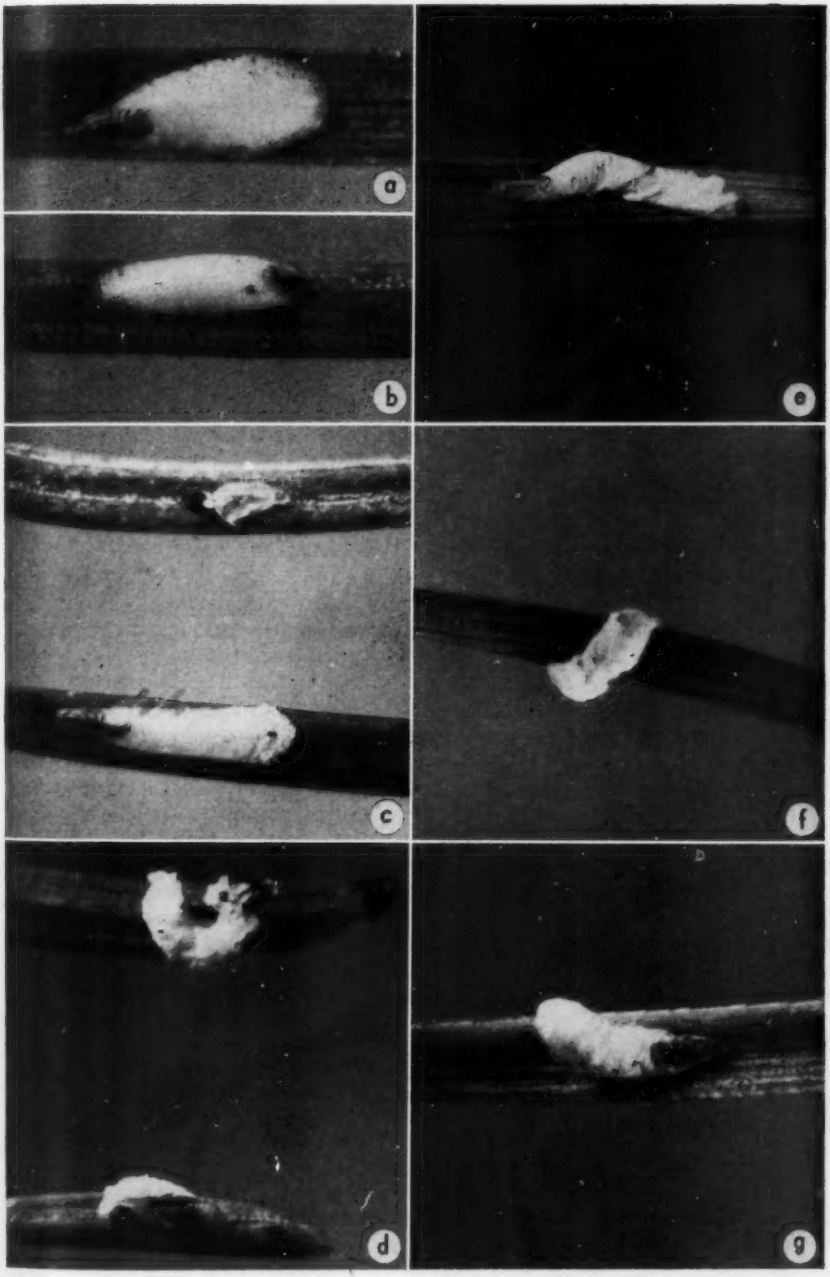

Fig. 2. Normal and abnormal scales of the pine needle scale. a, normal scale on pine; b, normal scale on spruce; c-d, abnormal scale on spruce; e-g, abnormal scale on pine.

TABLE II.

The incidence of egg laying females of the pine needle scale *Phenacaspis pinifoliae* (Fitch) when the males were excluded, Crowsnest Pass, Alta., 1957.

Sample No.	Total females	females which laid eggs		females not laying eggs	
		No.	Percentage	No.	Percentage
1	22	0	0	22	100
2	20	0	0	20	100
3	21	0	0	21	100
4	13	0	0	13	100
5	4	0	0	4	100
6	3	0	0	3	100
7	2	0	0	2	100
8	19	0	0	19	100
Total	104	0	0	104	—
Check	78	60	76.9	18	23.1

on lodgepole pine laid eggs and that mortality of both sexes was higher than at Indian Head.

Summary and Conclusions

A review of the literature shows that the following types of reproduction are found in the superfamily Coccoidea: (1) dioecious sexual reproduction, (2) obligatory parthenogenetic reproduction, (3) dioecious sexual reproduction with facultative parthenogenetic reproduction in the absence of males and (4) hermaphroditic reproduction. Scale insects which have normal dioecious sexual reproduction usually have a sex-ratio of one to one and in some species unfertilized females lay no eggs and produce abnormal scales.

Observations of the mating habits of the pine needle scale failed to show any strong sexual response by the females to the presence of the males. The males searched rapidly up and down the needles, passing over many females. They did not appear to have any means of orientating themselves for copulation when a suitable female was found.

The sex-ratio of the pine needle scale was approximately one to one in the populations examined. The initial experiment was designed so that the composition of the progeny of unmated females could be studied, but when the data were examined no consistent trends were established which would indicate an unusual number of either males or females in the progeny. The next experiments were inconclusive but gave some evidence that fertilization was necessary. None of the females in the last experiment laid eggs indicating that the pine needle scale, *Phenacaspis pinifoliae* (Fitch), is dioecious, that unfertilized females do not lay eggs, but produce abnormal scales and live much longer than those which have been fertilized.

Acknowledgments

The author gratefully acknowledges the help and guidance given to him by Dr. A. C. Hodson, of the Department of Entomology and Economic Zoology, University of Minnesota, under whose direction the first experiments were conducted. Data from unpublished records of previous work done on the pine needle scale at the Forest Biology Laboratory, Indian Head, Sask., were made available by Mr. L. O. T. Peterson, whose co-operation and assistance are gratefully acknowledged.

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(Received May 25, 1959)

Mortality of Cocoons of the Larch Sawfly, *Pristiphora erichsonii* (Htg.), in Relation to Distance from Small-Mammal Tunnels[1]

By C. H. BUCKNER[2]

Introduction

The relationship between the fate of cocoons of the larch sawfly, *Pristiphora erichsonii* (Htg.), and distance from small-mammal tunnels was studied during 1958 in the Whiteshell Forest Reserve of eastern Manitoba. The objects were to determine the distance that small mammals can detect cocoons and to observe possible effects of the interactions of small-mammal predation and other natural mortality factors of the insect. Additional analyses of the data provided information on the behaviour of the predators and the ecology of the prey insect.

Methods and Plot Descriptions

The ground vegetation in the study area consisted largely of sphagnum moss. The soil consisted of a layer of fibrous peat two to 12 inches deep underlain by limnic peat of considerable depth. Mammal tunnels were usually confined to the layer of fibrous peat. Attempts to follow mammal tunnels by digging resulted in a high degree of compaction of the moss and peat. It was soon realized that a high-speed cutting blade would be the only means of removing sections of this type of forest floor without compacting the moss and destroying evidence of tunnels. Accordingly, vertical transections of portions of the forest floor of the bogs were cut by means of a power chain-saw. The sections were two inches wide, extended downwards about two inches below the limnic peat, and varied

[1]Contribution No. 557, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

[2]Forest Biology Laboratory, Winnipeg, Manitoba.

TABLE I.

Summary descriptions of the five study plots, Whiteshell Forest Reserve, Manitoba.

Plot	Predominant tree species	Average height of trees (ft.)	Moisture conditions of forest floor	Predominant small mammal species
1	Black spruce Tamarack	40	Relatively dry	*Sorex cinereus cinereus* Kerr. *Clethrionomys gapperi loringi* (Bailey)
2	Black spruce Tamarack	12	Very wet	*Microtus pennsylvanicus drummondii* (Audubon & Bachman) *S. cinereus cinereus* Kerr.
3	Tamarack	40	Dry	*S. arcticus laricorum* Jackson
4	Tamarack	30	Wet	*Blarina brevicauda manitobensis* Anderson
5	Tamarack	30	Relatively dry*	*S. cinereus cinereus* Kerr

*The stand as a whole is very wet, but the area in which the samples were taken is as indicated.

in length from nine inches to about four feet, depending upon the topography. Each section was laid on a board as it was cut and the profile mapped. Small-mammal tunnels appearing on the surface of the cut were superimposed upon the profile drawing and then the deeper tunnels were opened with a pair of six-inch scissors and sketched on the map. Major topographic features, such as the level of the limnic peat, the level of the water table, and the positions of large roots, were added to the map.

The moss was then sorted with the least possible disturbance to the section. Sawfly cocoons, both new and old, were located and classified by categories as listed in Table II. Other insects, especially dipterous puparia, were treated similarly.

Five plots were studied in this experiment. Plots 1, 2, and 3 have been described previously (Buckner, 1957). Plot 4 was located near Red Rock Lake and Plot 5 between White and Betula Lakes. Table I lists the important features of each plot, as well as the most abundant species of small mammals determined from four years of trapping.

The area of the sections was measured with a planimeter and the volume of moss sampled was calculated. The length and volume of the tunnels were measured. These data are recorded in Table II.

TABLE II.

The extent of moss sampling on each plot, and the relationship between moss volume and the intensity of small-mammal tunnelling.

Plot	No. sections	Area of sections (sq. ft.)	Volume of sections (cu. ft.)	Length of tunnels (ft.)	Volume of tunnels (cu. ft.)
1	15	8	3	91	0.14
2	28	10	4	156	0.19
3	59	26	16	621	1.56
4	12	5	2	77	0.09
5	40	21	8	313	0.44

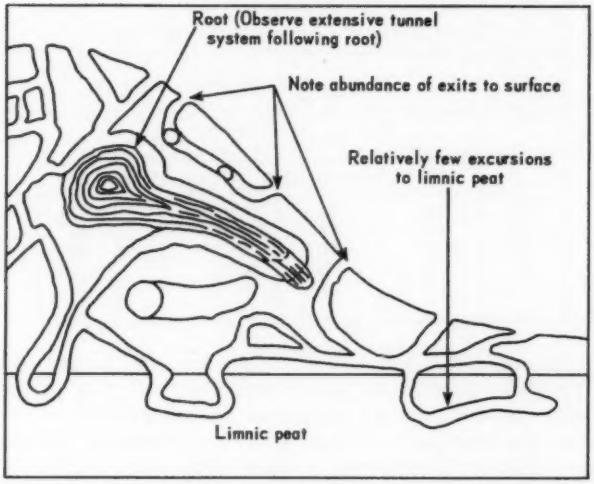
Root (Observe extensive tunnel system following root)
Note abundance of exits to surface
Relatively few excursions to limnic peat
Limnic peat

Fig. 1. Typical moss profile showing small-mammal tunnels.

The Structure of Small-Mammal Tunnels

After very few sections had been removed for examination it was evident that the moss was virtually honeycombed with tunnels (Table II). A surprising observation was the frequency of branch tunnels to the surface of the moss. These occurred at intervals of about six inches (Fig. 1). Most tunnels were well defined, and it was apparently possible to distinguish between tunnels constructed by long-tailed shrews and those constructed by other small mammals. The former were about one-half inch in diameter and about one-half the diameter of the latter. Relatively few tunnels occurred in the depressions of the bogs compared with the number occurring in the hummocks. There was conspicuous absence of tunnels through ant nests. When a tunnel reached a root it often ran parallel to it for distances up to four feet.

Five large chambers littered with the remains of cached sawfly cocoons were found. It was often possible to predict the finding of a chamber by the scarcity of cocoons in the surrounding area. Sawfly emergence was entirely unsuccessful among these cached cocoons, suggesting that once a cocoon has been found and cached it can be considered as being destroyed. The five caches contained a total of 158 cocoons ranging in number from 17 to 42. Of the cocoons found in caches, 11 were sound, 26 had parasite emergence holes, 14 were dead, two were opened by rodents, and 105 were opened by long-tailed shrews.

Differences in Mortality Between Plots

Each cocoon was classified as sound, emerged, parasitized by *Bessa harveyi* Tnsd., dead, attacked by insect predator, or attacked by small mammals. Cocoons opened by small mammals were further classified as attacked by long-tailed shrews (chiefly *Sorex* spp.), attacked by *B. brevicauda*, or attacked by rodents (chiefly *C. gapperi*, and *M. pennsylvanicus*). The opening in the cocoon provided a reliable criterion of its fate (Buckner, 1957; Morris, 1949). The mortality sources of larch sawfly cocoons are given in Table III. Mortality was lowest

TABLE III.

Fate of larch sawfly cocoons of the study plots.

Plot	No. cocoons examined	Percentage of cocoons by categories							
		Sound	Emerged	*Bessa harveyi* emergence	Dead	Attacked by insect predators	Opened by *Sorex*	Opened by *Blarina*	Opened by rodents
1	719	7	10	17	9	5	23	1	28
2	1304	2	14	3	5	2	39	2	11
3	6371	3	12	10	5	2	49	5	12
4	291	13	30	5	11	1	15	25	0
5	754	2	8	8	11	8	35	8	2

on Plot 4 where predation by small mammals was also lowest. On Plots 2, 3, and 5, the long-tailed shrews are usually abundant, and it is on these plots that small mammals exert the greatest impact upon the larch-sawfly cocoon population, thus illustrating the importance of these small insectivores as predators of this insect. Rodents destroyed the largest number of cocoons on Plot 1 and substantially augmented mammalian predation on Plots 2 and 3, suggesting that at times they too can aid in the natural control of the larch sawfly.

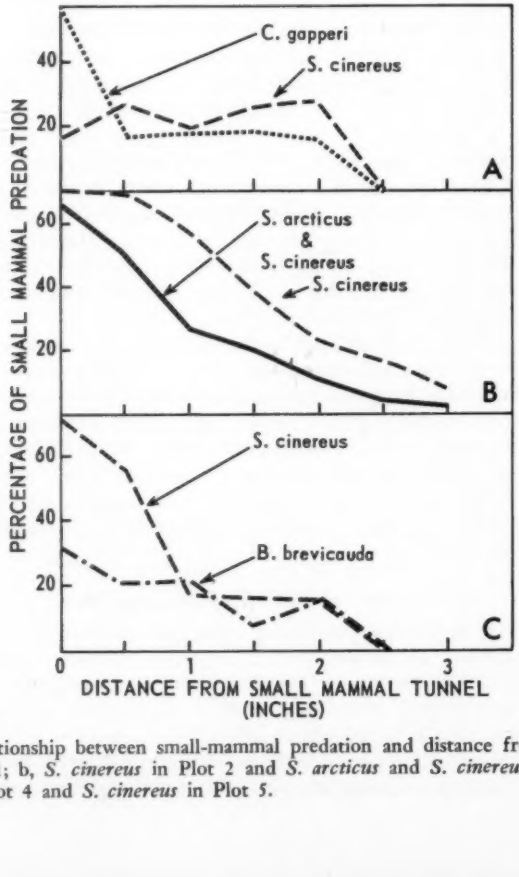

Fig. 2. Relationship between small-mammal predation and distance from small mammal tunnels. a, Plot 1; b, *S. cinereus* in Plot 2 and *S. arcticus* and *S. cinereus* in Plot 3; c, *B. brevicauda* in Plot 4 and *S. cinereus* in Plot 5.

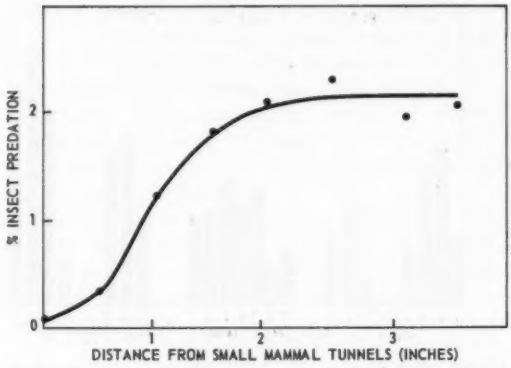

Fig. 3. Relationship between destruction of cocoons by insect predators and distance from small-mammal tunnels.

Destruction by insect predators was the only other mortality factor recorded. This varied from one to eight per cent but again no obvious relationship to site characteristics was observed.

Unexplained mortality in the cocoon stage varied between plots but no obvious relationship to any environmental factor was evident.

Emergence of the tachinid parasite *B. harveyi* varied from plot to plot, being highest on Plot 1 and lowest on Plots 2 and 4. There appears to be a relationship between the success of *B. harveyi* and the moisture content of the forest floor.

Small-Mammal Predation in Relation to Small-Mammal Tunnels

The percentage of small-mammal predation was considered in relation to the distance of the cocoon from the nearest mammal tunnel. Cocoons within the tunnel were called zero distance, and thereafter cocoons were grouped at half-inch intervals. The results are shown in Fig. 2. With the exception of that for Plot 1, the curves are similar in shape. Predation was high in the tunnel and rapidly declined beyond the first inch. At three inches from the tunnels predation was negligible. It appears that most of the predation occurs in the one-inch zone immediately surrounding the tunnel.

It has been pointed out (Morris, 1949; Holling, 1955, 1958; Buckner, 1955, 1958) that some small mammals do not feed indiscriminately on sawfly cocoons, but reject in varying degrees those cocoons whose contents are unpalatable. Cocoons containing dead sawflies and some species of parasites were in the unsuitable category. Accordingly, the cocoons in successive half-inch zones from small-mammal tunnels were analysed with respect to mortality and emergence of *B. harveyi* (Figs. 4, 5). In all cases the percentage of dead cocoons was low in the tunnels, high in the area close to the tunnels and low in areas more remote from tunnels. Each plot was analysed separately for significance by $2 \times n$ chi-square tables (Snedecor, 1946). All these differences were significant at the one per cent level (Chi-squares 16.307, 33.197, 56.561, 14.858, 21.235 — d.f. 3, 2, 6, 2, and 3 respectively). These differences are probably a result of selectivity of the mammalian predators, which may carry a few dead cocoons to the tunnels but seldom open them. Mortality is apparently high close to the tunnel because a higher proportion of sound cocoons is either eaten or removed from this site by small mammals. Mortality in the outer zones is probably

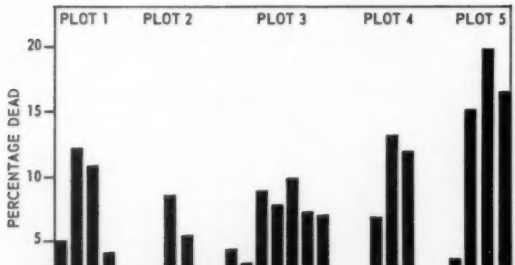

Fig. 4. Mortality of larch-sawfly cocoons in relation to distance from small-mammal tunnels.

representative of the condition existing in the absence of small mammalian predators.

If all small mammals rejected cocoons parasitized by *B. harveyi*, the percentage of emergence of *B. harveyi* should be low in the tunnel, high in the zone surrounding the tunnel and lower in zones more remote from the tunnel. Fig. 5 shows that this is not always the case. The differences on Plots 1, 2 and 5 were significant at the one per cent level (chi-squares 20.125, 16.182, 13.075 respectively – d.f. 3, 2 and 3 respectively) but were not significant on Plots 3 and 4 (chi-squares 5.726 and 5.537 respectively – d.f. 6 and 2 respectively). On Plot 1 the predominant mammalian predators were *C. gapperi* and *S. cinereus*, and on Plots 2 and 5 the predominant predator was *S. cinereus*. In laboratory experiments these species have demonstrated the ability to reject cocoons parasitized by *B. harveyi*. On Plots 5 and 4 the predominant mammalian predators were *S. arcticus* and *B. brevicauda* respectively, both of which failed in laboratory experiments to discriminate between healthy and parasitized cocoons. Thus the results in Figs. 4 and 5 are in accordance with the known behaviour of the predator concerned.

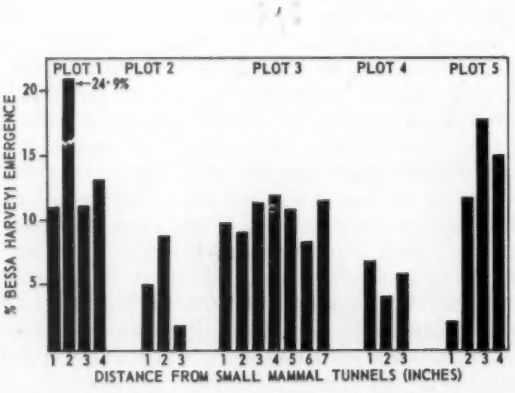

Fig. 5. Emergence of parasite *Bessa harveyi* Tnsd. in relation to distance from small-mammal tunnels.

Mortality of larch sawfly cocoons by insect predators may also be related to the proximity of the cocoons to the tunnels. However, the relatively small number of cocoons that fell into this category makes comparisons inconclusive. On this plot the percentage of cocoons destroyed by insect predators increased in an outward progression from the tunnels (Fig. 3) and the difference was significant at the one per cent level (Chi-square 15.057, d.f. 6). This may indicate predation by soricids on the insect predators themselves whenever they are encountered in or near the runways.

Other faunal remains encountered during the study were also recorded. The majority of these were puparia of *B. harveyi* and other Diptera. Of the 929 dipterous puparia found, only one showed evidence of predation by small mammals. Buckner (1957), gave evidence that dipterous puparia are unpalatable to most small mammal predators.

Cocoon Mortality in Relation to other Topographic Features

The study lends itself to an investigation of mortality of cocoons in relation to features of the topography other than small-mammal tunnels. Two such features are the depth below the surface of the moss and the height above the limnic peat.

When the distribution of cocoons is plotted according to depth below the surface there are no significant differences in the percentage of mortality factors except on Plot 1 where a significantly higher percentage of cocoons was destroyed by soricids in the uppermost inch layer (77 per cent in the top layer and 70 per cent in the remainder with a chi-square of 6.501 with one degree of freedom; significant at the one per cent level). Possibly this explains the peculiar relationship between cocoons destroyed by *S. cinereus* and the distance from tunnels shown in Fig. 3. Even the difference is not widely divergent from the mean. Excepting Plot 1 the data agree with those obtained by the cocoon-planting technique, suggesting that predation is independent of depth (Buckner, 1958).

When cocoon mortality is considered in relation to height above the limnic peat, there is in general no significant difference, with one notable exception. The percentage of emergence of the parasite *B. harveyi* was significantly lower as one approached the limnic peat on Plots 2 and 4 as shown in Fig. 6. Chi-squares were 10.947 with 3 degrees of freedom and 14.716 with 3 degrees of freedom (both significant at the one per cent level), respectively. These plots are wet, and it is reasonable to assume that cocoons in the vicinity of the limnic

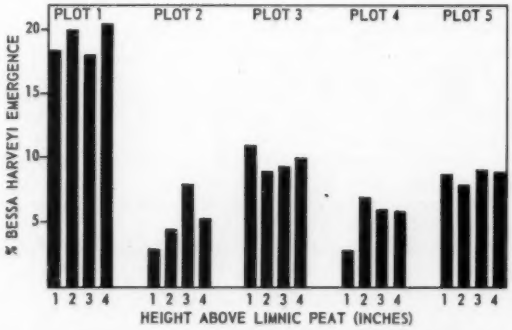

Fig. 6. Emergence of *Bessa harveyi* Tnsd. in relation to the proximity to the limnic peat.

peat are subject to inundation during the fluctuations of the water table. Assuming that the percentage of cocoons containing *B. harveyi* is the same at all distances from the limnic peat, the data lend support to laboratory experiments by Heron (1959) who found a successive increase in mortality of developing *B. harveyi* maggots with increasing exposure to submergence.

Summary

1. Small-mammal tunnels were very abundant in the bogs studied. Entrance holes to the surface occurred at about six-inch intervals. Five subterranean chambers were found and these contained caches of larch sawfly cocoons.
2. Small mammal predators usually destroyed over 50 per cent of the larch sawfly cocoons. Mortality due to small-mammal predation was lowest in an area where *Blarina brevicauda* was the predominant predator and highest where *Sorex cinereus* was predominant. The majority of larch-sawfly cocoons were destroyed within an inch of the tunnels. At three inches from the tunnels small mammals almost ceased to be a mortality factor.
3. Evidence suggests that small mammals reject dead and parasitized cocoons. The percentage of dead cocoons was low in the tunnels, high in areas close to tunnels, and lower again in areas more remote from tunnels. The percentage of successful emergence of the parasite *Bessa harveyi* showed a similar trend where *Clethrionomys gapperi* and *Sorex cinereus* were abundant. Both these predators had previously been shown to reject parasitized cocoons. No relationship was found between the percentage of successful emergence of *B. harveyi* and the distance from tunnels in areas where *Sorex arcticus* and *B. brevicauda* predominated. Both these predators failed in previous experiments to discriminate between healthy and parasitized cocoons.
4. Except in one area, small-mammal predation was found to be independent of the depth of the cocoons.
5. Most dipterous puparia had not been opened by small mammals, indicating that these are unpalatable to most mammalian predators.
6. Successful emergence of *B. harveyi* was highest on the dryer sites. In wet areas the percentage of emergence of *B. harveyi* was lower as the limnic peat was approached. These data suggest that mortality of the parasite is higher in wet situations.

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Observations on a "Complex" of Insects in Tops of Black Spruce in Manitoba and Saskatchewan[1]

H. R. Wong, J. A. Drouin, and B. B. McLeod[2]

Introduction

Stands of black spruce, *Picea mariana* (Mill.) B.S.P., in Northern Manitoba and Saskatchewan were defoliated by insects from 1954 to 1955 (Prentice and Hildahl, 1955). The defoliation was sufficient to show reddening of the tops from the ground as well as from aircraft at an elevation of 1,000 feet. Collections showed clearly that the most abundant species was the black-headed budworm, *Acleris variana* (Fern.); larvae could be found at all crown levels. Other species of insects were also common in the tops of trees with dense compact foliage such as often found in "club-tops" of black spruce. The reddening of foliage was not noticeable after the decline of the black-headed budworm populations in 1956, but the numbers of the other insects, which formed a "complex" of species, persisted at varying levels of abundance in the tops of black spruce.

Many species of insects were collected from black spruce tops and reared at the Winnipeg Laboratory. The five most abundant species were identified by Drs. T. N. Freeman, D. F. Hardwick, and E. Munroe, of the Entomology Research Institute in Ottawa, as follows: *Herculia thymetusalis* Wlk., *Archippus alberta* (McD.), *Epizeuxis americalis* (Gn.), *Dioryctria abietivorella* (Grote) and *Recurvaria* sp. Two other species collected less frequently were *Gerdana caritella* Busck and *Zeiraphera fortunana* Kft.

Infested tops of black spruce are characterized by a mass of dense foliage, cones, and larval webbing, in which is lodged large quantities of frass, dried needles, and parts of damaged cones (Fig. 4). This seems to form an ecological niche for the "complex" of insect species. The feeding damage is cumulative from year to year, and it is impossible to ascertain the degree of damage that can be attributed to each species. Their relative abundance and feeding habits, however, are established. These are discussed below.

Relative Abundance and Feeding Habits

Recurvaria sp.

Collections from the tops of black spruce totalled 226 in 1955 and 1956. These show trends in the relative abundance of the principal species with the exception of *Recurvaria*. Because of its small size, larvae often were overlooked in the early collections, and the proportion of this species in collections probably is underestimated (Table I).

This species is responsible for most of the mined needles in the upper crown. Under laboratory conditions it feeds on current foliage (Fig. 5), and overwinters as a larva in mined needles. In spring needle-mining and the webbing together of damaged needles, frass, and bits of bud scales is continued.

Herculia thymetusalis Wlk.

This is the most abundant species collected. The number of larvae obtained in both years was more than twice that of *A. alberta* (Table I). The penultimate and ultimate instars of *H. thymetusalis* have been described by Brown and McGuffin (1942). Larvae overwinter in silken cases, which are spun in masses of frass, old needles and cones, and in the spring feeding is resumed on the old

[1]Contribution No. 544, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

[2]Forest Biology Laboratory, Winnipeg, Manitoba.

TABLE I

Relative abundance of insect species in the tops of black spruce based on 226 collections and 1,813 larvae in Manitoba and Saskatchewan in 1955 and 1956.

Insect species	Percentage of species	
	by collections	by larvae in collections
Herculia thymetusalis Wlk.	60	45
Archippus alberta (McD.)	47	19
Recurvaria sp.	26	12
Dioryctria abietivorella (Grote)	21	9
Epizeuxis americalis (Gn.)	14	3

foliage. Larvae also feed on new foliage as it becomes available. In some cases the more mature larvae were observed feeding on the bud scales and the outer surface of young cones. It is possible that feeding habits change with instars. Laboratory observations and field collections in late December indicate that this species overwinters in several instars.

Archippus alberta (McD.)

Under laboratory conditions larvae feed on new foliage. They web a number of needles together and feed within this shelter. The winter is apparently passed in the larval stage in mined needles.

Dioryctria abietivorella (Grote)

This species has been described by MacKay (1943) and Craighead (1950) as *D. abietella* (D. & S.). Recent studies by Munroe (1959) indicated that the Nearctic *D. abietivorella* (Grote) is different from the Palaearctic *D. abietella* (D. & S.) and should not have been synonymized with the latter. Although *D. abietivorella* is not numerous (Table I), it causes conspicuous damage to the cones. Larvae may feed on the surface of young cones or tunnel into them. Because of its boring habits it damages both scales and seeds (Fig. 6). It has also been noted feeding occasionally on needles in the laboratory. When feeding on cones, the larval frass tends to be reddish brown, in contrast with greyish-green frass when feeding on foliage. The larva overwinters in a silken cocoon constructed in September and October.

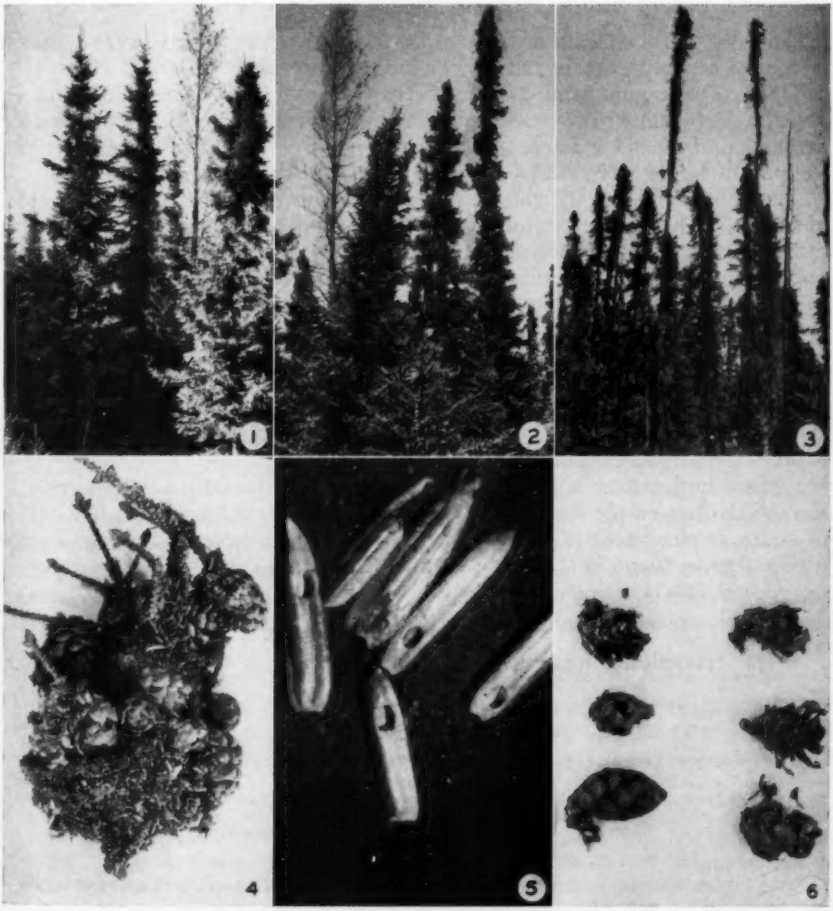
Epizeuxis americalis (Gn.)

Populations of this species generally are very low, with one or two specimens being frequently collected in a sample. It passes the winter in the larval stage, and resumes feeding in the spring mainly on the old foliage. The ecological niche in the tops of black spruce is similar to the one described by Craighead (1950) and Crumb (1956) who reported this insect occurring in the nests of squirrels and ants.

Distribution in Trees and Stands

A sampling method was used in 1956 to determine the distribution of defoliation and cone damage within the crowns of black spruce. Sample trees were selected at five locations in Saskatchewan, and four in Manitoba. After the sample trees were felled, branches were removed from the lower, mid, and upper crowns. All insects were removed from the sample branches and reared for identification. Cone damage and defoliation of old and new foliage in sample branches were conspicuous only in the uppermost crown level. Larvae were similarly collected only from those sample branches taken from the upper crown.

It is obvious from Table I that not all the black-spruce tops sampled contained these insects. After it was established that these insects were mainly confined to the top three feet of the upper crown, it became apparent that some crown types supported greater numbers of insects than others. Proof of this was attempted by tallies made in a five-acre plot near Prince Albert National Park. This plot covered an area of swamp and sloping terrain, with a ridge rising some 25 feet above the level of the swamp. The stand in the swamp consisted largely of black spruce from about 100 to 150 years old and from four to six inches d.b.h., interspersed with tamarack. A mixture of black spruce and jack pine occurred on the slope and ridge; the spruce on these two sites were about 60 to 90 years old and from five to eight inches d.b.h. Fifty spruce trees were



Figs. 1-6. Crown classes, needles, and cones of black spruce attacked by a "complex" of insect species. 1, Trees with conical or open crown. 2, Trees with slender or intermediate crown. 3, Trees with "club-top" or dense upper crown. 4, Branch removed from infested top showing mass of frass, webbing, and damaged needles and cones. 5, Needles damaged mainly by *Recurvaria* sp. 6, Cones damaged mainly by *Dioryctria abietivorella* (Grote).

TABLE II

Percentages of defoliation and damaged cones to black spruce trees by crown types, Bittern Creek, Sask., 1957, based on 162 branches from 27 trees.

Crown type	Per cent defoliation		Per cent of cones attacked
	old foliage	new foliage	
Conical	1	1	3
Intermediate	5	1	9
Club-top	15	4	27

tallied along a line on each of the three sites. The upper crowns were classified as conical or open-growing, slender or intermediate, and "club-top" (Figs. 1, 2, and 3). At the same time 27 trees of each crown class were felled, and six branches were removed from the upper crown. The branches were examined for defoliation of the old and new foliage as well as the percentage of cones damaged. Samples of larvae were reared for confirmation of species present.

As shown in Table II, "club-top" crowns tend to support the largest numbers of insects. The per cent defoliation of foliage and cone damage was highest in this crown type. Intermediate or slender crowns maintained a much smaller population followed by conical crowns. This is indicated by the reduction in damage to foliage and cones. The preference of the "complex" of species is apparently one of density of foliage, cones and branches. This condition is provided mainly by black spruce trees with "club-top" crowns, to a lesser extent intermediate crowns, and occasionally conical crowns. There is no indication that feeding of these insects actually causes the "club-top" condition commonly found in black spruce. This condition is apparently due to tree vigour, which is probably correlated with site and maturity.

Black spruce trees with "club-top" crowns were found more frequently in the swamp than on the slope, and less frequently on the ridge (Table III). This of course implies that the largest populations of the "complex" of species can be expected to be found in the swampy or slow-growing sites, which was supported by general observations over the entire region.

Geographic Distribution

The "complex" of insect species was collected as far north as limits of

TABLE III

Percentages of crown types of black spruce trees, Bittern Creek, Saskatchewan, 1957, based on 50 trees on each site.

Site	Per cent of trees with		
	Conical crown	Intermediate crown	"Club-top" crown
Ridge	54	32	14
Slope	14	52	34
Swamp	0	22	78

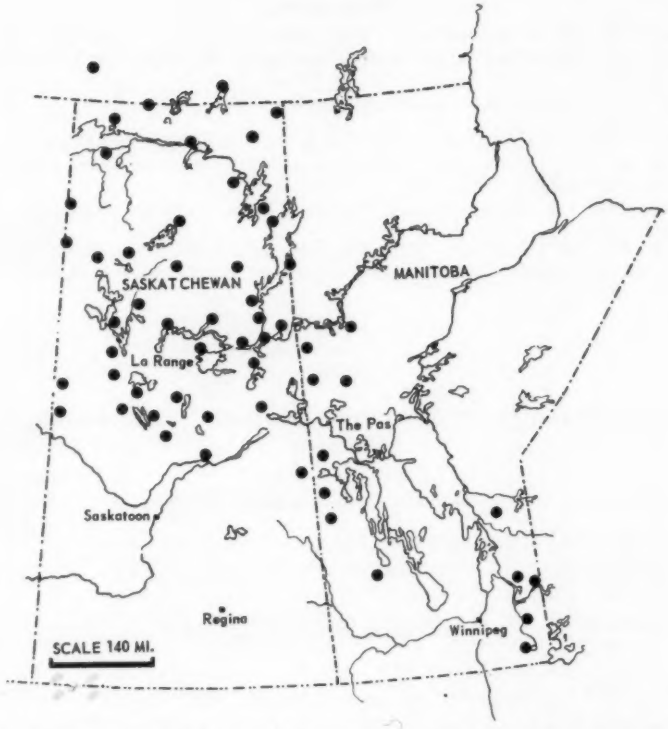


Fig. 7. Locations in Manitoba and Saskatchewan where the foliage and cones of black spruce trees were attacked by a "complex" of insect species.

observations in 1954 and 1955, which was roughly the 59th parallel in Saskatchewan and the 57th parallel in Manitoba as indicated in Fig. 7. Subsequent surveys have recorded the "complex" as far north as the 61st parallel in the Northwest Territories. There is little doubt that the community of insects reported herein covers the full range of black spruce in the two provinces.

Field Guide to the "Complex" of Species in the Tops of Black Spruce

A study on the life history of some of the species is proposed, with descriptions of larvae. In the meantime a rapid method for identifying these species in the field should be helpful. The following simple key was prepared for this purpose.

1. Head reddish-brown in colour 2
   Head brownish in colour 3
2. Body yellowish-brown with 5 dark longitudinal lines on dorsum *Herculia thymetusalis* Wlk.
   Body greyish-olive green without longitudinal lines on dorsum ..... *Archippus alberta* (McD.)
3. Body with reddish dorsum and yellowish venter ..... *Recurvaria* sp.
   Body purplish-brown or reddish-brown 4
4. Body purplish-brown with three faint longitudinal lines on dorsum .....
   Dioryctria abietivorella (Grote)
   Body light reddish-brown with black tubercles on dorsum and black spiracles .....
   Epizeuxis americalis (Gn.)

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Seasonal Variation of Tabanids (Diptera) in Algonquin Park, Ontario[1]

By D. M. DAVIES[2]
McMaster University, Hamilton, Ontario

Horse flies and deer flies were collected throughout the spring and summer of 1955 by the author and others in the vicinity of the Wildlife Research Station, Algonquin Park, Ontario. These collections include 2,712 females of 15 *Chrysops* species, three males and 278 females of 13 *Tabanus* species and one female of *Stonemyia tranquilla* (O. S.). However, tabanids collected in other years from the Park have been studied as well[3]. In 1955 *T. trepidus* McD. (35%) and *T. epistates* O. S. (15%) together accounted for half the *Tabanus* species collected, and *C. vittata* Wied. (23%), *C. montana* O. S. (16%) and *C. wiedemanni* Kröber (15%) for more than half the species of *Chrysops* (Table II).

In Algonquin Park tabanids were first observed on the wing in late May to mid-June in different years, one to four weeks later than simuliids and at almost the same time as, or slightly later than, *Culicoides* (Table I). The genus *Chrysops* in some years appeared one to two weeks earlier than the genus *Tabanus*.

Although the 1955 collections in Algonquin Park were made in different places and by various methods, the total number of each species collected each week was compared throughout the season (Figs. 1 and 2). Active collecting continued from May 21 to August 13, except for a less active period from June 18 to June 26, when none were collected, although collectors were in the field on five of these days. Of the species of *Chrysops*, *C. mitis* O. S. and *C. excitans* Wlk. appeared to be the earliest in 1955, and *C. montana*, *C. shermani* Hine, *C. vittata* and *C. wiedemanni* the latest (Fig. 1 and Table II). One female of *C. wiedemanni*, the only tabanid seen in the first two weeks of September, was collected by D. M. Wood on September 18. The earliest species of the genus *Tabanus* in 1955 were *T. lasiophthalmus* Macq. and *T. nudus* McD., and the latest *T. typhus* Whitney and *T. microcephalus* O. S. (Fig. 2 and Table II).

In 1955, the first peak of *Chrysops*, mainly *mitis, inda* O. S., *excitans* and *cuclux* Whitney, occurred on June 6 (Fig. 1) when the maximum air temperature

[1]Contribution of Department of Biology, McMaster University, supported by a grant from National Research Council of Canada.

[2]Associate Professor of Zoology.

[3]I wish to acknowledge the help of Dr. B. V. Peterson, Dr. A. M. Fallis and D. M. Wood who made their collections available to me, and that of Brian Poole and Dr. L. L. Pechuman who did most of the identifications.

rose to 80°F., several degrees more than the maximum of the previous few days. On June 15, a similar peak occurred, involving mainly *excitans, mitis* and *inda* but also *cuclux, celer* O. S. and *shermani*. On the same day the number of brown *Tabanus*, mainly *T. trepidus* Mc.D., *T. epistates* and *T. affinis* Kirby, increased at least five times that of the previous day. This was coincident with a sharp rise in daily mean temperature from 55°F. to 66°F. with a maximum

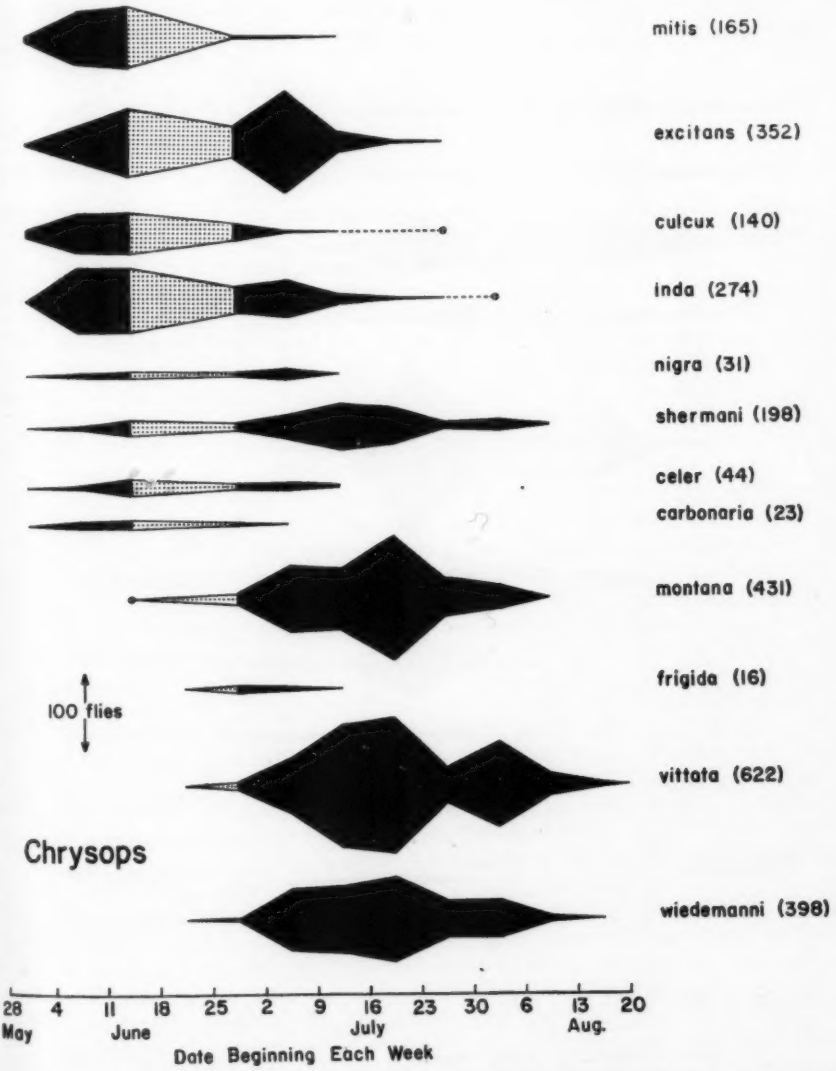

Fig. 1. The seasonal change in the abundance of different species of *Chrysops* in Algonquin Park, Ontario, as shown by the total catch per week in 1955. The number of specimens for each species is in parentheses. *One *C. weidemanni* was taken on September 18.

temperature close to 80°F. At the beginning of July the number of grey *Tabanus*, mainly *T. typhus*, began to increase accompanied by a definite decrease in the number of brown *Tabanus*. However, the grey species of *Tabanus* appeared to be more restricted to the lakeshore than the brown species, and as most collecting was done farther from the water, the actual collections reflect less strongly this change from brown to grey *Tabanus* species. *C. montana* showed a sharp increase at the beginning of July followed a few days later by a marked increase in *C. vittata* and *C. wiedemanni* and a resurgence of *C. excitans*.

Data from other years (1937-1956) indicated that some species of *Chrysops* and *Tabanus* might have a much longer span of activity than they did in 1955

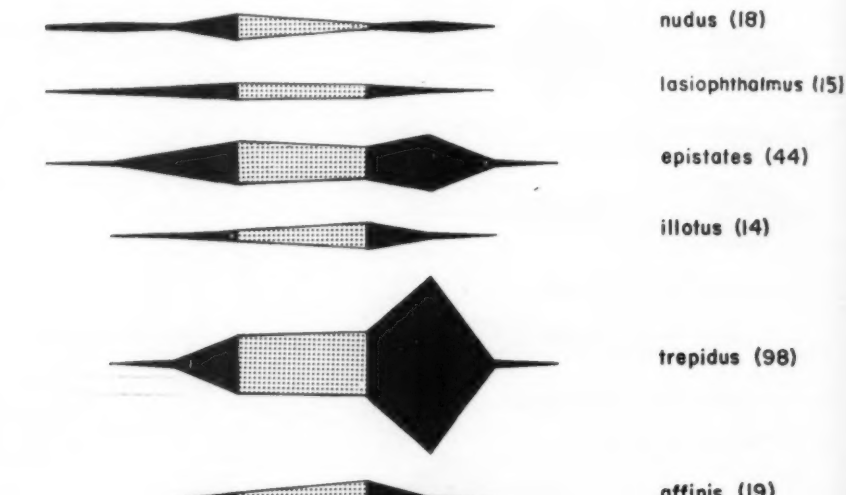

Fig. 2. The seasonal change in the abundance of different species of *Tabanus* in Algonquin Park, Ontario, as shown by the total catch per week in 1955. The number of specimens for each species is in parentheses.

TABLE I.

Earliest Flying of some Bloodsucking Insects in Algonquin Park, Ontario.

Year	Tabanidae		Ceratopogonidae	Simuliidae
	Chrysops	Tabanus	Culicoides*	—
1947	23V1	30V1	15V1	16V (8V)**
1948	7V1	20V1	—	30V ***
1949	23V	11V1	—	13V (30?V)
1950	6V1	12V1	5V1	8V (8V)
1951	2V1	2V1	26V	17V ***
1955	26V	26V	4V1	3V

*Mainly *C. obsoletus* Mg.
**Emergence date in brackets.
***Probably occurred earlier.

(Table II). The data on seasonal distribution in Algonquin Park are compared with those from other localities. However, differences in seasonal distribution may result partly from early to late seasons in different years, as well as from the differences in locality. The records for two species of *Chrysops*, *C. carbonaria* Wlk. and *C. frigida* O. S., common to both Churchill, Manitoba (Miller 1951) and Algonquin Park indicated that their span of adult activity was one month later in the northern site. Three species of *Tabanus* (*affinis* Kirby, *frontalis* Wlk. subsp. *septentrionalis* Lw. and *zonalis* Kirby) began 12 to 14 days later at Churchill in 1947-1949, than the same species in Algonquin Park. In Goose Bay, Labrador a few tabanids (*T. metabolus* McD. and *C. excitans*) appeared first about June 25 in 1952 and 1953, and *C. carbonaria* and *T. zonalis* were abundant in July, but *T. typhus* and *T. astutus* O. S., beginning in mid July, were the only species persisting into August, numbers occurring on August 10 (Brown and Morrison 1955). This indicates that tabanid activity may occur at about the same time there as at Churchill, or about one month later than in Algonquin Park. The records from New York State (Stone 1930, Tashiro and Schwardt 1950, Pechuman 1957) and Connecticut (Fairchild 1950) showed that most tabanid species were active at the same time to a week earlier than in Algonquin Park, but several species appeared to begin adult activity at a later date than in Algonquin Park. In Tennessee in 1953 (Pechuman 1954), *T. nigripes* Wied. was active almost two weeks earlier than in Algonquin Park in 1955. Only one female of *T. minusculus* Hine was collected from the Park, on August 2, 1937, but Judd (1957) found it to occur from June 25 to August 25, 1956 in Byron Bog, near London, Ontario. Records from Quebec indicate that most species of *Chrysops* and *Tabanus* are active in June and July but that adults of *C. vittata* and *C. wiedemanni* are found also in August and those of *T. lasiophthalmus* also in May (Chagnon and Fournier 1943).

A few observations were made in Algonquin Park on the hosts on which various species fed. More horse flies than deer flies were attracted to large objects such as cars and buildings and possibly deer; the ratio of *Tabanus* to *Chrysops* from inside cars was at least twice that around humans. *Chrysops montana*, *C. vittata* and *C. wiedemanni* were among the species biting humans in June and July. The attack of *T. nivosus* O. S. on the lower legs, ankles and feet was frequent from July 7 to 21, 1955. This species appeared to fly from 1 to 2 feet above the ground and was much more frequent over marshes, beaches and even at the rocky shores of lakes. *T. microcephalus* and *T. zonalis* also

showed this tendency to fly low and to dwell near water. Five females of *C. mitis* and one of *C. cuclux* were taken on June 10, 1955, while feeding on two recently killed deer (*Odocoileus virginianus borealis* (Miller)) and two females of *C. vittata* were probing with their mouthparts. Often species of *Tabanus* (e.g., *nudus*) were netted with their ventriculi filled with blood possibly from deer as there were no horses or cattle in the area. A female of *C. montana* was taken on June 21 in the Park as it fed on a collie dog. Miller (1951) reported

TABLE II.

A Comparison of the Seasonal Occurrence of Some Adult Tabanidae in Algonquin Park, Ontario and in New York State (percentage of each species in the collections made in 1955 in Algonquin Park, Ontario forms the first column; T = less than 1%).

	%	Algonquin Park		Ithaca, N.Y.[d,f] New York State[f]
		1955	1937–1956	
Stonemyia tranquilla (O. S.)	T	14VII	14VII	VII (VIII)[e]
Chrysops				
carbonaria Wlk.	1	6VI–6VII	6VI–8VII	mid V–end VI
celer O. S.	2	6VI–10VII	6VI–10VII	late V–end VI
cuclux Whitney	5	2VI–29VII	2VI–29VII	late V–mid VI
excitans Wlk.	13	28V–22VII	28V–14VIII	mid VI–end VI
frigida O. S.	1	27VI–11VIII	27VI–4VIII	(V) VI–early VII(IX)[e]
inda Osten Sacken	10	3VI–2VIII	3VI–2VIII	mid VI–mid VII
laterlis Wied.	T	30VI–4VII	30VI–4VIII	VI into VIII[e]
mitis O.S.	6	28V–7VII	28V–10VII	V until VII[d]
montana O.S.	16	16VI–8VIII	16VI–13VIII	start VII–early VIII
nigra Macquart	1	4VI–8VII	4VI–30VII	late V–mid VII
shermani Hine	7	4VI–10VIII	4VI–17VIII	late VI into VIII[e]
sordida O. S.	T	3VI–10VI	3VI–28VI	VI–VIII[e]
venus Philip	T	16VI–7VII	16VI–19VII	—
vittata Wied.	23	28VI–13VIII	21VI–18VIII	late VI–end VIII
wiedemanni Kröb.	15	28VI–18IX	28VI–18IX	late VI–mid VIII
	100			
Atylotus thoracicus (Hine)	T	—	early VII[a]	VII (VIII)[e]
Tabanus				
affinis Kirby	7	15VI–4VII	11VI–8VII	start VII–end VII
astutus O. S.	–	—	10VIII	VIII[d]
criddlei Brooks	–	—	28VI[b]	—
epistates O.S.	15	2VI–14VII	2VI–14VII	first 3 wks. VII
rontalis Wlk. subsp. *septentrionalis* Lw.	–	—	22VI	VI–VIII[d]
illotus O. S.	5	5VI–8VII	5VI–8VII	(V) mid–late VI(VII)[e]
laspiophthalmus Macq.	5	28V–3VII	28V–3VII	(mid V–mid VII (28V–14VII[f]
microcephalus O.S.	3	13VII–22VII	13VII–22VII	start VII–end VIII
minusculus Hine	–	—	2VIII[c]	3VII; VI–VIII[e]
nigripes Wied.	2	6VII–12VII	6VII–12VII	—
nivosus O. S.	4	28VI–18VII	28VI–14VIII	late VI–early VII
nudus McDunnough	6	26V–4VII	26V–4VII	VI into VII[e]
reinwardtii Wied.	T	15VII	15VII–24VII	late VI–early VIII
trepidus McD.	35	6VI–12VII	6VI–4VIII	late VI–mid VII
trispilus Wied.	7	29VI–7VII	29VI–4IX	mid VI–end VIII
typhus Whitney	10	27VI–22VII	27VI–22VII	(VI) VII (VIII)[e]
zonalis Kirby	1	29VI–3VII	21VI–15VII	VI and VII[e]
	100			

[a]1944. Bella lake, 10 m. west of Algonquin Park (Miss S. M. Whittemore).
[b]1956. Wildlife Research Station, Algonquin Park (D. M. Wood).
[c]1937. Algonquin Park (A. M. Fallis).
[d]1925-1928. (Stone, A., 1930).
[e]A number of years. (Pechuman, L. L., 1957).
[f]1948-1949. (Tashiro, H. and Schwardt, H. H., 1953).

husky dogs as well as humans being severely bitten by *T. affinis* and *T. frontalis* subsp. *septentrionalis* (as *T. septentrionalis* Lw.) at Churchill, Manitoba. One female of *T. illotus* O. S. was netted on June 11 while it rested on one of two eggs in a loon's nest (*Gavia immer*) at the water's edge. One female of *C. excitans* was induced to feed on a domestic Pekin duck (*Anas* sp.) on July 9, 1948. The ducks were adept with their bills in capturing and eating *Chrysops* flying near their heads and seldom would flies feed naturally on them. Dr. G. F. Bennett (*in litt.* 1959) collected species of *Chrysops* that were feeding naturally on a raven (*Corvus corax*) and a crow (*Corvus brachyrhynchos*) in Algonquin Park. He also observed that certain species of *Chrysops* but none of *Tabanus* fed on a domestic Pekin duck, when they were enclosed with it in a fine-mesh cage. These observations of tabanids feeding on birds are of special interest as Oldroyd (*in litt.* 1958) said that Tabanidae are not recorded as feeding on birds.

One of two female *Chrysops* (*C. inda*) was netted on the sunny morning of June 11, 1955 as they hovered over a flower of the yellow pond lily (*Nuphar advena* (Ait.)). They may feed on the nectar of this flower.

Records of predators and parasites of tabanids are few so that it is of interest to report that the bald-faced hornet (*Vespula maculata* (Linn.)) was commonly observed in Algonquin Park feeding on *Chrysops* that gathered in the top of a white canvas tent. Also a larval trombidiid mite was seen on the proximal end of the forefemur of a female *Tabanus tepidus* on June 28, 1955 and one on a female of *T. nivosus* in early July 1955.

Summary

The first appearance of tabanids in each of the several years in Algonquin Park, Ontario is compared with that of *Culicoides* and simuliids. For certain tabanid species, the period of their seasonal occurrence in Algonquin Park is compared with that in other parts of central and eastern Canada and United States. The change in seasonal abundance of species of *Chrysops* and *Tabanus* is illustrated for 1955 in Algonquin Park. A few observations of tabanids feeding on mammals and birds are mentioned.

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Egg-laying Habits of Lepidoptera in Relation to Available Food

By V. G. Dethier

Zoological Laboratory, University of Pennsylvania,
Philadelphia 4, Pennsylvania

Introduction

Entomologists interested in population dynamics have devoted considerable attention to the numbers of eggs laid by various species of insects, the mortality and non-viability of eggs, and mortality in young larvae; but there is another aspect of the problem which has received less attention than it deserves. This is the necessity for females to place their eggs sufficiently close to an adequate supply of food to insure the growth and development of the F_1 generation. Fulfillment of this requirement is particularly important for those species whose larvae are restricted feeders, that is, monophagous or oligophagous. It is generally assumed that the continued existence of a species is evidence that the eggs are always properly placed. As a consequence of this assumption very few quantitative studies have been undertaken, with the result that the contribution of the adult's behaviour to the degree of survival in larval populations is unknown. The following field studies were undertaken to supply some information on this score.

Precision in Oviposition

In our admiration of the unerring skill with which certain moths and butterflies select for oviposition just that plant upon which the larvae will feed, we are inclined to overlook the fact that many species either do not practice this skill or, if possessed of it, frequently err. It has been pointed out by Dethier (1953), for example, that the European argynnid, whose larvae feed only on *Viola*, customarily oviposits upon the trunks of trees and that many skippers (Hesperiinae) lay their eggs on non-edible substrates or even in some instances drop them in air. Noctuids, hepialids, and satyrids have been reported by Portier (1949) as dropping eggs in flight. According to Van Son (1955) the butterfly *Dira clytus* scatters eggs indiscriminately in grass. " . . . while the female is stationary on a blade of grass; they are first laid and then shot away." Villiers (1957) described certain females as deliberately letting eggs roll to the ground at the foot of food-plants. Examples of failure to oviposit directly on the proper plant can be multiplied from personal experience or from the literature. It will suffice to give quantitative data on six species. The African swallowtail *Papilio demodocus* is generally meticulous in laying its eggs on *Citrus*, one of the principal larval food-plants. However, a female watched for a period of two hours was observed to lay ten eggs, of which one was placed on *Citrus* and nine on minute sticks, pebbles, and grasses, often as far away as 15 feet from the nearest tree. None of the grasses chosen were fed upon by the larvae. Another African species, *Danaus chrysippus,* which in the larval stage is restricted to Asclepiadaceae, over a period of one hour laid twenty eggs, of which ten were placed on the proper food-plant, in this case small asclepiad seedlings, and the remainder on pebbles or grains of sand. Van Son (1955) reported that this species occasionally lays eggs on vegetation nearby the food-plant. The egg-laying habits of two of the mimics of *D. chrysippus* were also observed. One, the nymphalid *Hypoliminas misippus,* laid four of ten eggs on soil instead of on the seedlings of its food-plant, *Sedum.* The other mimic, the papilionid *Papilio dardanus,* laid seven of eleven eggs on the ground instead of on its food-plant, *Citrus.* A Cuban skipper, *Pyrgus syrichtus* Fabr., placed every one of eight eggs on different *Sida* plants. *Sida* was unacceptable to the larvae (Dethier, 1940).

A Cuban nymphalid, *Anartia lytrea chrysopelea* Hbn. placed equal numbers of eggs on *Tradescantia* and *Lippia.* The former was unacceptable to the larvae (Dethier, 1941).

It is not to be implied from these observations that precision in choice of food-plant by the ovipositing female is not common. In many hours of observation the following species were never seen to err: *Vanessa virginiensis* Drury on *Gnaphalium, Precis zonalis* Felder & Felder on *Lippia, Danaus plexippus* on *Asclepias, Pieris rapae* on Cruciferae.

Taken in the sum, however, these observations indicate that precision is neither absolute nor invariable and that there is no obvious correlation between the degree to which the larvae are restricted to specific plants and the accuracy with which the adult oviposits.

The lack of precision in egg laying by species whose larvae are restricted feeders represents behaviour of questionable adaptive value. Compensation for the deficit rests with the larvae. In the older literature the statement was made frequently that larvae did not require a refined sense of discrimination or ability to search effectively for food because the egg-laying habits of the adults obviated this necessity. In many of the species already discussed this is clearly not the case. Furthermore, in many species where the female does indeed exhibit more precision in these matters the need for larval abilities is nonetheless acute because a number of these species oviposit upon minute seedlings which are insufficient for complete development. Two examples will suffice to illustrate this point. An ovipositing individual of *Vanessa virginiensis* Drury was observed over a period of two hours. This female was laying eggs on seedlings of everlastings (*Gnaphalium*) which were growing in a gravel driveway. The smallest of these was one centimeter in its longest dimension; the largest covered an area of nine square centimeters. Continued observations during the period of larval growth in the weeks that followed confirmed the impression that *in no case* was the seedling sufficiently large to support the growth of a larva beyond the second instar, especially since the larva grew faster than the seedling. Similar observations have been made with a number of species, including the following Cuban butterflies: *Metamorpha stelenes insularis* (Holland), which oviposited on exceedingly small seedlings of *Blechum blechum; Nathalis iole* Bdv., which oviposited on minute seedlings of *Bidens leucantha.* It would appear, therefore, that in those species whose larvae are monophagous or oligophagous and restricted to herbaceous plants, survival and the success of the population depends in no small measure upon the discriminative and dispersal activities of the larvae.

Numbers of Eggs in Relation to Food-plant Distribution

The need for dispersal and food-plant recognition is especially acute in gregarious species which are herbaceous feeders, since the single plant upon which such colonies feed seldom constitutes a sufficient food supply. This is true, for example, of the butterfly *Melitaea harrisii* Scud. (Dethier, 1959). It is strikingly illustrated by *Euchaetias egle* Drury and *Nudaurelia dione* Fabr. (even though this species feeds on bushes and small trees) in the following examples.

Euchaetias egle Drury is a North American arctiid moth which lays its eggs in clutches of ten to one hundred or more on species of milkweed (*Asclepias*) and on dogbane (*Apocynum androsaemifolium* L.), to which the larvae are rigidly restricted for feeding (cf. French, 1884). They feed both night and day and are gregarious in all instars but will feed if placed alone on a plant. They pupate singly in which stage they over-winter.

TABLE I.

Dispersal of lavae of *E. egle* from food plant.

Date	Time	Plant number																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
August 2		217																
3		217																
4	(rain)																	
5	0900	0																
	0915	0	2	4														
	1000	0	19	4														
	1030	0	19	20	29	3	0	1	1	0								
	1115	0	21	31	44	5	1	0	1	5	1	2						
	1300	0	20	37	47	5	1	0	1	6	12	3	18					
	1445	0	22	37	47	6	1	1	1	6	16	1	21					
13		0	25	1	0	6	1	0	11	2	10	14	1	1	2	1	12	8
19		0	25	1	0	6	1	0	11	2	10	14	1	1	2	1	12	8

On August 2 a colony consisting of two clusters of 121 and 96 larvae was found on a dogbane plant (Fig. 1, plant No. 1), where they were in the process of molting into the third instar. The plant had been completely skeletonized. Twenty-four hours later, all had molted successfully and had become very restless. On August 4, two had left the plant and were seen in the vegetation about two feet away traveling away from the sun. By 11:00 P.M., August 4, it was raining heavily. All of the larvae were extremely active on the plant but were not leaving it. By 9:00 A.M. of August 5 all had deserted the plant. They were crawling in all directions on the surrounding vegetation. Nothing gave a more striking appearance of randomness; however, more were moving at right angles to the sun than at any other direction. By 9:15 two had found and ascended a nearby plant (Fig. 1, No. 2). By 10:00 there were 19 on plant No. 2 and four on plant No. 3. The majority were now moving in a direction roughly at right angles to the new sun position. The subsequent distribution of this colony until August 19, when they dispersed to pupate, is given in Table I. During this period the most distant plants populated were one located 24 feet south of the home plant and another located nine feet west. At the time of pupation there were 95 survivors, or about 44 per cent of the original population. It was observed that many of the larvae while wandering between plants became entangled in spider webs and were killed. Others fell prey to ants and other species of spiders. The longer they remained on the ground, the greater their chances of eventually being killed by predators. Within a radius of 200 feet of the colony there were in excess of 1,000 dogbane plants, none of which bore larvae.

Nudaurelia dione Fabr. is a large African saturniid moth which lays its eggs in small clusters much like the North American cecropia moth. The female lays a total of about 200 eggs. The species is polyphagous; however, the larvae do show marked feeding preferences (Rougeot, 1949). In a case studied in the Belgian Congo there were, in an area 25 feet square, 35 *Ricinus* plants 18 feet high. On two of these there were 217 larvae in the penultimate instar which

Fig. 1. Map showing the location of seventeen dogbane plants. Eggs of *E. egle* were laid on plant No. 1, and larvae eventually migrated to all plants shown. The scale indicates distance in inches.

15
14
13
11
9
10
17
16
12
3
4
2
1
5
8
7
6
0
30

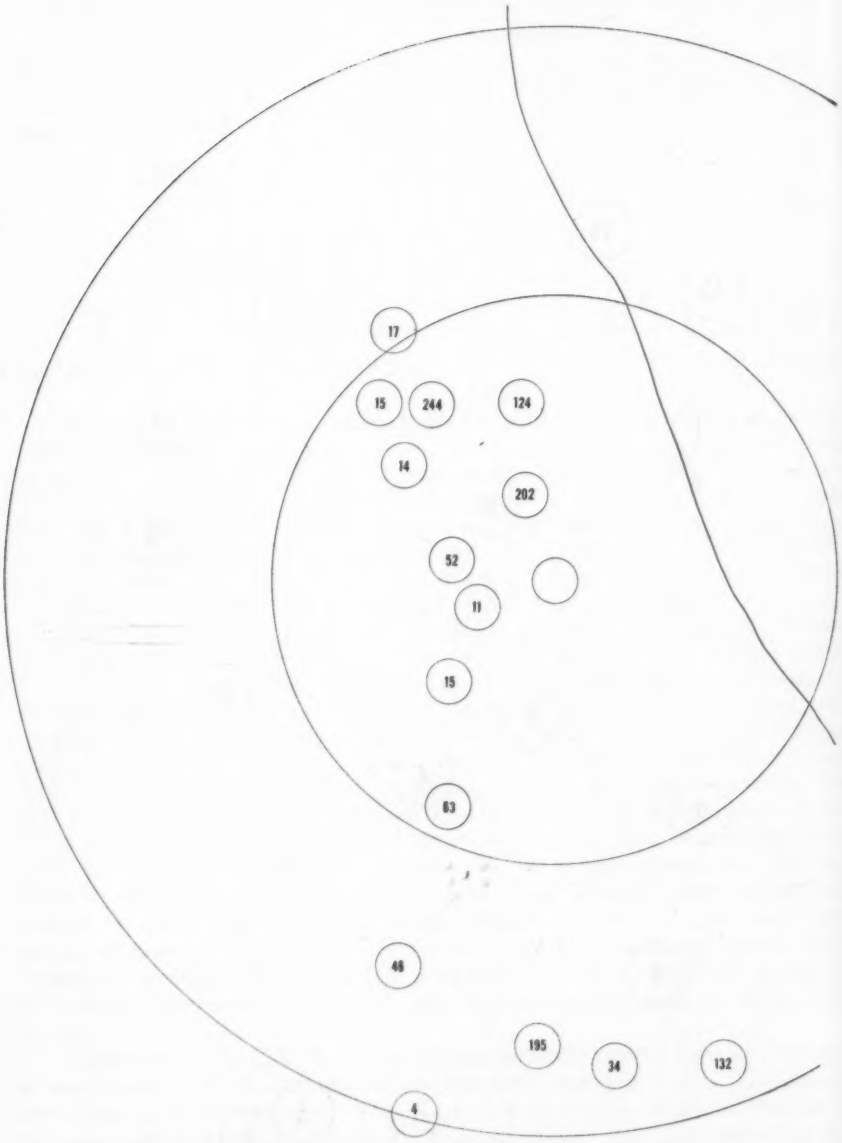

Fig. 2. Distribution of groups of *Ricinus* plants within a radius of one kilometer of the laboratory. The numerals refer to the number of plants in each group. The empty circle marks the location of the two plants bearing 217 larvae of *N. dione*. The only other larvae in the area were four in group 11 and thirty-four in group 244. The irregular line marks the shore of Lake Tanganyika.

had completely defoliated both. The larvae were extremely active crawling over the denuded trees and many nearby objects, including a papyrus, a guava, and a papaya. A *Ricinus* nine feet from the home plant was untouched, although another 12 feet away had been reached by an overhead bridge. Two larvae were attempting to eat guava. None of the larvae in this colony succeeded in pupating. A survey of *Ricinus* within a radius of 1.0 km. of this group showed that there were 966 plants. Their distribution is shown in Fig. 2. Of these one had four larvae and another 34. Thus there were a total of 38 larvae in an area containing 966 trees, yet the 217 by virtue of being confined to trees were lost to the species.

A comparable case involved eight larvae of *Charaxes* sp. which completely defoliated a small legume and succumbed to starvation, although several yards away there was an adequate supply.

The relation between total amount of food available to a population and the amount actually used is strikingly illustrated by the following observations.

Rhodophora florida is a striking little pink North American noctuid moth which lays its eggs singly on the stalks and calyx of flowers or on very young pods of the evening primrose, *Oenothera* (Fitch, 1868; Saunders, 1869, 1871; Dickerson and Weiss, 1920). The solitary larvae feed day and night on the contents of the pod. Winter is passed in the pupal stage.

Evening primroses in the area were restricted to a 150-foot stretch of road (Fig. 3) and a nearby banking on the shore. In 1956 the total number of flowering evening primroses in these two areas was 38. Only nine moths were caught and marked during that summer. Daily observations revealed that these moths seldom strayed from the vicinity of evening primroses. This adult population produced a total of 51 larvae which were confined to 12 of the 38 evening primroses. The maximum number of larvae on any plant was five. The number of pods per plant averaged 15, with a maximum of 24 per plant and a minimum of four. There was clearly no relation between the number of pods and number of larvae per plant (See Table II). Larvae on eight of the 12 primroses were marked with distinctive colors. Until they completed their growth, they never left the plant. In two cases where they depleted the food supply they finally abandoned the plant but failed to find another 12 inches away.

The following summer only three moths were found in this area. The total number of larvae produced was 31. These were distributed as shown in Fig. 3 on nine of 38 plants.

TABLE II.

The number of larvae of *R. florida* on primroses in relation to the number of pods per plant.

Number of pods per plant	Number of larvae per plant
11	5
22	3
23	2
17	5
24	4
6	1
7	0
13	1
20	0
12	2
10	1
16	5
20	3
4	1

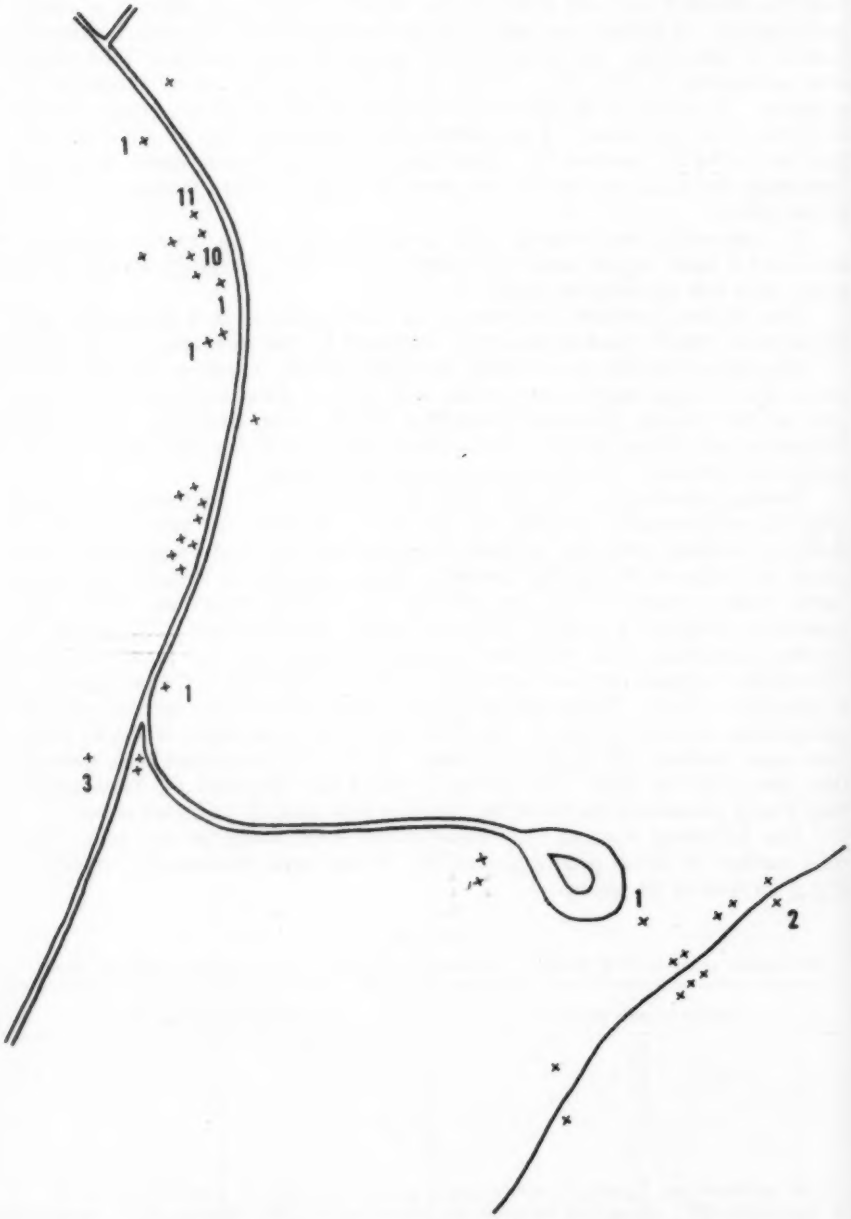

Fig. 3. Distribution of primrose plants along a 150-foot stretch of road in a coniferous forest. The numerals refer to the number of individual larvae of *R. florida*. The irregular line indicates a bank at the edge of the ocean.

As with the other species discussed, the larval population of *R. florida* in the area is much lower than that which could be supported by the primroses. Here, however, the instances in which a plant constitutes an inadequate supply of food for the completion of development are few. The total number of eggs laid in terms of the adult population is small.

Conclusion

Studies in losses of eggs and young in insects have usually emphasized mortality arising from disease, predation, non-viability, and adverse environmental conditions. The foregoing examples indicate that errors made by adults in the selection of oviposition sites may contribute appreciably to losses. While the absolute number of eggs characteristically produced by a species is one factor which must be taken into consideration in population studies, the distribution of eggs in relation to the size, number, and spatial arrangement of foodplants is another factor which may be of considerable importance.

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History of the Alfalfa Weevil, *Hypera postica* (Gyll.) (Coleoptera: Curculionidae), in Alberta

By G. A. Hobbs[1], W. O. Nummi[2], and J. F. Virostek[2]
Crop Insect Section, Canada Agriculture Research Station
Lethbridge, Alberta

In June, 1954, the alfalfa weevil, *Hypera postica* (Gyll.), was found in very small numbers (one per 500 sweeps) in alfalfa fields in the valley of the Milk River and in the area between the hamlets of Onefour and Orion in southeastern Alberta. These were the first records of its occurrence in Canada. As the host-specific parasite *Bathyplectes curculionis* (Thoms.) (Townes and Townes, 1951) emerged from some of the weevil larvae collected then, the weevil had been in Alberta for at least one year. On July 26 an intensive search was made in the irrigated areas around Lethbridge. Only two weevils were taken in approximately 25,000 sweeps from 25 fields. The distribution of the weevil at this time indicated that it had migrated from the irrigated areas of Montana that lie along the lower reaches of the Milk River by way of the river valley.

Although the weevil was not of economic importance in the one county in Montana in which it was established in 1940 (Hamlin, McDuffie, and Lieberman, 1949), it had become a major pest in the south-central counties by 1948 (Hastings and Pepper, 1949). By 1952 it had become an economically important pest in at least a part of Phillips County (Pepper, 1953), which is bounded on the north by Canada and through which the Milk River flows. By 1954 the weevil was established along the northern border of Montana on approximately a 300-mile front opposite Alberta and Saskatchewan (Pepper, 1954). Unpublished reports from Montana have indicated that, in general, the weevil became economically important about 10 years after establishment in an area.

Surveys to determine distribution and spread in Alberta were carried out from 1955 to 1958. To facilitate planning control measures if the weevil became economically important, four of the fields in which it had been found in 1954 were surveyed at regular intervals in 1957 and 1958 to determine seasonal history and to assess population trends and parasitism by *B. curculionis*. Three of the fields were in that part of the Milk River valley east of longitude W 112°, and the fourth was at the Canada Agriculture Range Experiment Station, Manyberries.

Methods

To determine distribution and spread in Alberta, 500 sweeps per field were taken in alfalfa fields throughout the irrigated regions of southern Alberta; each set was taken as the sweeper walked diagonally across the field. To determine seasonal history and to estimate numbers of larvae and parasitism, sweeps were made as above at regular intervals when overwintered adults of their larvae were active in the four fields selected. In 1958, the number of sweeps per field was decreased as the number of larvae increased; at the peak number of larvae only 30 sweeps per field were made. The larvae from half of the sweeps were reared to the prepupal stage to determine the percentage of parasitism, and the remainder were preserved in 70 per cent ethyl alcohol for later calculations of the percentages of each instar present. The ranges of widths of head capsules determined by Hamlin *et al.* (1949) for each instar were used to indicate stage of development. Head widths of 50 larvae chosen at random from each catch from each field were measured. Because sweeping apparently did not dislodge nearly as many of the early-instar larvae, which feed in terminal growth, as of

[1]Entomologist, [2]Assistant Technician.

the late-instar larvae, data for first and second instars are omitted from the table on stages of development of larvae.

Results and Discussion

Spread and Increase of the Weevil in Alberta

By 1956, the weevil was found in all alfalfa fields examined south of the St. Mary's, Oldman, and South Saskatchewan rivers in Alberta. In 1957, for the first time, the weevil was found north of these rivers near Hays. In 1958 a few sweeps were enough to obtain it in alfalfa fields in the Scandia area of the Eastern Irrigation District north of the Bow River. Surveys north of this area were not made.

The peak numbers of larvae taken in sweeps in the three fields in the Milk River valley and the one at Manyberries were:—

	Year				
	1954	1955	1956	1957	1958
Larvae/sweep	0.002	0.40	0.92	2.65	48.00

They increased slowly from 1955 to 1957 and sharply in 1958. From 1957 to 1958, numbers of overwintered adults increased from an average of one per 17 sweeps to one per four sweeps.

These findings suggest that once the weevil is established it spreads rapidly throughout an area. Migration is not caused by population pressure as numbers per sweep remain very low until after all of the fields in an area are infested. Then numbers per sweep rise faster perhaps because further diffusions within an area result in reinfestations from more and more points.

Economic Importance

Damage was inconspicuous, even in the field at Manyberries where 60 larvae per sweep were taken; it was not known whether there was sufficient damage to warrant application of control measures. In Montana, Hastings and Pepper (1953) reported that as few as 35 larvae per sweep at first cutting time were associated with about a 15 per cent reduction in total yields of hay from the three cuttings taken that year.

Seasonal History

Average numbers of larvae per sweep taken in the four fields were:—

1957	May 10	June 3	June 17		July 2
	0.0	0.3	1.8	—	2.6
1958	May 22	June 5	June 16	June 23	July 2
	0.0	4.0	19.5	48.0	16.0

In the spring the adults apparently became active late as no weevil larvae were obtained on May 10, 1957, or on May 22, 1958, although the alfalfa averaged eight and 11 inches in height, respectively; furthermore, in 1957 more overwintered adults were swept on June 3 (119 per 2,500 sweeps) than on May 10 (14 per 2,000 sweeps) However, larvae increased rapidly in number from then on (leader table above) and they were in about the same stage of development at first hay cutting time as they were in Utah (cf. Hamlin *et al.*, 1949). For example, the alfalfa field at Manyberries was cut for hay on June 20, 1958, three days before peak numbers were counted on the three fields in the Milk River valley (leader table above), and when about 55 per cent of the larvae were in the fourth, or final, instar (Table I); it might have been cut for hay on or before June 16, when only about 35 per cent were in the fourth instar. As the percentage of larvae in the fourth instar was over 90 on July 2, 1957 (Table I), the peak in numbers of larvae probably occurred sometime between June 17 and

TABLE I

Percentages of larvae of the alfalfa weevil in third and fourth instars on various dates in four of the fields in which it was originally found

Year	Day	3rd instar	4th instar
1957	June 3	75	6
	June 17	57	33
	July 2	9	91
1958	June 5	37	12
	June 16	46	36
	June 23	28	71
	July 2	24	74

July 2; hence, peak numbers for 1957 were probably higher than indicated in the above leader tables.

Parasitism by B. curculionis

B. curculionis was not as important in Alberta in 1958 as it was in Utah during the period 1930-1932 (cf. Hamlin *et al.*, 1949); the highest percentage of parasitism for any one date of collection was 53. As in Utah, the percentage of parasitism was highest in the earliest-hatching larvae. Only 16 per cent of the weevils were parasitized on June 23 when peak numbers of larvae were recorded, and 24 per cent on July 2. The total parasitized evidently remained about the same throughout the larval period of the weevil; as the numbers of larvae increased, the percentage of parasitized decreased and vice versa. Adults emerged in the laboratory in July from about 10 per cent of the parasite cocoons from larvae swept on June 5 and 16, 1958; according to Hamlin *et al.* (1949), this partial second generation parasitized some late-hatching larvae in some years.

In Utah (Hamlin *et al.*, 1949), *B. curculionis* destroyed most of the larvae that reached the fourth instar before the first cutting; according to them, only fourth-instar larvae survived the destruction of their food and shelter. As few overwintered adults remained to lay eggs in the new growth, the early-hatched larvae that escaped parasitism contributed the major portion of the next year's population. Hence, the severity of succeeding infestations depended largely upon the number of unparasitized larvae that reached the fourth instar before the first hay crop was cut. If parasitism should increase as weevil densities increase, it may be possible to control the weevil in Alberta by cutting the first crop for hay when most of the larvae are immature and when most of those that develop early are parasitized.

Summary

The number of alfalfa fields in which the alfalfa weevil was found in Alberta increased from a few in the area south of the Oldman and South Saskatchewan rivers in 1955 to all those examined in the irrigated areas of southern Alberta in 1958. The average numbers per sweep found in four of the fields that were infested in 1954 rose from 0.002 to 48 in 1958, the greatest increase occurring in 1958. Although the adults became active in the spring apparently later in relation to the development of alfalfa in Alberta than was reported for Utah, the larval populations increased and developed rapidly and reached about the same stage of development at first cutting time as did those in Utah. Parasitism by *B. curculionis* was not nearly as high in southern Alberta as reported for Utah,

perhaps because the weevil was still comparatively scarce; as in Utah, the parasite has a partial second generation.

Acknowledgments

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A new species of *Casinaria* from British Columbia (Hymenoptera: Ichneumonidae)

By G. Stuart Walley

Entomology Research Institute, Research Branch, Canada Department of Agriculture
Ottawa, Canada

Recent rearings of the geometrid *Melanolophia imitata* (Wlk.) by officers of the Vernon and Victoria, B.C., laboratories of the Forest Biology Division, Canada Department of Agriculture, have yielded a series of a new species of *Casinaria* for which the following description is offered.

***Casinaria melanolophiae*, new species**

Female. Length 7 mm. Head thin, temple rather weakly receding for a considerable distance behind eye, and beyond rather strongly rounded to occiput; antenna with 29-31 segments, the shortest flagellar segments at least a little longer than broad; cheek short, about 0.30 breadth of base of mandible; ocelli large; greatest diameter of lateral ocellus twice as great as ocellocular space and three-fourths as great as post-ocellar line; head and thorax dullish, with granular sculpture; mesoscutum and scutellum densely, shallowly punctate, with punctures somewhat obscured by granular sculpture; sides of thorax finely granular and with only a few minute punctures; propodeum and abdomen as in *C. semiothisae* Wly.

Black. Apex of scape narrowly yellowish; pedicel yellowish beneath; middle femur and to a lesser extent front femur usually more or less suffused with fuscous beneath; coxae, basal segment of hind trochanter, hind femur and all tergites of abdomen, black; in other respects with color as in *C. semiothisae*.

Male. Length 6 mm. Antenna with 30 segments; front coxa usually yellowish at apex; structure and color otherwise much as in female.

Holotype. ♀, Quadra Island (Sayward District), B.C., July 11, 1958. Forest Insect Survey, No. 58.752.03A.

Paratypes. 5 ♂♂, 17 ♀♀, from the following British Columbia localities: Alberni, Campbell River, Corrigan Creek, Cortes Island, Cowichan Lake, Elk Falls, Franklin River, Genoa Bay, Henderson Lake, Iron River, Kootenay River, Jervis Inlet, Narcosli Creek, Nile River, Qualicum, Roberts Lake, Sproat Lake, Stamp Falls, and Westbridge.

Except for a few specimens that emerged out of season, in the laboratory, and two unusually late (Sept. 8 and 13) emergents, the above material was reared on various dates in July and August in the years 1950-53, and 1958.

Holotypes and paratypes, No. 6840, in Canadian National Collection. Paratypes in United States National Museum and Townes Collection.

Cocoon. Length 6.5 mm., diameter 2.5 mm. Whitish, marked near each end with an annulus of elongate blackish spots, also with a few small blackish spots on ends.

Host. All specimens in the type series were reared from *Melanolophia imitata* (Wlk.).

Distribution. Central and southwestern British Columbia.

Most of the specimens studied were obtained from localities in a restricted area embracing the eastern slope of central and southern Vancouver Island and adjacent islands in the Strait of Georgia. A few records from the interior of British Columbia (Kootenay River, Narcosli Creek, and Westbridge) indicate that the species may be generally distributed in the central and southern regions of the Province.

Remarks. This species belongs in the structurally compact "*scabriformis* group" of *Cavinaria*, as defined in my previous synopsis (Sci. Agr. 27: 364, 1947), where it most closely resembles *C. semiothisae* Wly. In most respects it agrees in structure with *semiothisae*, from which it differs in color, however, in the blackish hind femur and the uniformly black abdominal tergites. In addition it differs from *semiothisae*, and also from *C. eupitheciae* Vier., in the color and maculation of the cocoon. In the latter two species the cocoon is brownish-black, with a narrow, sordid greyish median annulus, whereas in *melanolophiae* it is whitish, with blackish spots.

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Gross Effects of Some Pesticides on Populations of Phytophagous Mites in Ontario Peach Orchards and Their Economic Implications

By W. L. PUTMAN AND D. C. HERNE

Entomology Laboratory, Research Branch, Canada Department of Agriculture, Vineland Station, Ontario

Since 1946, a major project at the Vineland Station laboratory has been one on the indirect effects of pesticides on populations of injurious arthropods in peach orchards of the Niagara Peninsula. Plant-feeding mites have been the most readily affected. This paper describes the gross changes in mite populations produced by the pesticides and considers their economic importance and the possibility of reducing their injurious effects. The controversial problem of the means whereby some pesticides, particularly DDT, promote mite increase is still under study and will be treated in later papers.

Ripper (1956), in his review of the effects of pesticides on the balance of arthropod populations, cited many examples of increases of phytophagous mites following the use of certain pesticides. Outbreaks of the European red mite, *Panonychus ulmi* (Koch), have occurred so widely on other fruit crops treated with DDT that their occurrence on peach was to be expected. Driggers (1946) and Hamilton (1949) reported such outbreaks on peach in the United States, and Targe (1954) in France. Wheeler and LaPlante (1946) and Hamilton (1949) found that increased infestations of the two-spotted spider mite, *Tetranychus telarius* (L.), followed the use of DDT on peach. A number of authors, including Barnes (1951) in California and Lord (1956) in Nova Scotia, reported increases of the "clover" mite, i.e., forms of the *Bryobia praetiosa* Koch complex, following the use of DDT in apple orchards; in most cases the species concerned was probably the brown mite, *B. arborea* Morgan and Anderson.

Strains of the European red mite resistant to parathion were first reported by Newcomer (1951), O'Neil and Hantsbarger (1951), Newcomer and Dean (1952), and Lienk, Dean, and Chapman (1952) on apple, and subsequently by many others.

No references were found in the literature on effects of fungicides on mites in peach orchards, but various authors have reported such effects in apple orchards. Lord (1949), among others, found that sulphur promoted increase of the European red mite in Nova Scotia. Miller (1953) found that captan produced increases of this mite in Tasmania, and Morgan, Anderson, and Swales (1958) found the same effect in British Columbia.

The toxicity of sulphur to mites of the *Bryobia praetiosa* complex has long been known; Weldon (1909) was among the first to present experimental evidence from orchards. Anthon (1954) found sulphur to be the most toxic of several materials tested against the peach silver mite, *Vasates cornutus* (Banks).

General Methods

The investigations were carried on in mature commercial peach orchards owned by Messrs. G. Janzen, J. A. High, and W. D. Troup in Louth Township, Lincoln County; in the Victoria and Boothman orchards at the Ontario Horticultural Experiment Station, Vineland Station; and in a younger orchard at the Plant Pathology Laboratory, St. Catharines. All were on good peach soil. The Janzen, High, and Troup orchards were bounded on three sides by peach or other orchards usually sprayed with DDT and sometimes rather heavily infested with the European red mite. The other orchards were bounded on not more than

one side by sprayed trees. The orchards were usually divided into approximately square plots of 100 or more trees, or about one acre. As the orchards were seldom large enough to hold more than one plot per treatment the effects of replication were achieved as far as possible by conducting similar experiments in two or more orchards or by rearranging the positions of the plots after a period of time. Unfortunately such methods did not lend themselves to statistical analysis. In some of the later work, smaller plots of 30 to 60 trees were used, and randomized single trees on one occasion, adjacent trees being protected from spray drift by large sheets of cotton held on poles.

From 1946 to 1951 all materials were applied as dilute sprays by means of high-pressure outfits with hand guns. From 1952 to 1957 the larger plots were sprayed with concentrates applied by an automatic mist blower, the amounts of pesticides applied per acre being equivalent to those that would have been applied as dilute sprays. Dilute sprays were still used in some of the smaller plots.

Materials used were 50 per cent DDT wettable powder from various sources; 15 per cent parathion wettable powder from various sources; wettable sulphur containing 95 per cent or more elemental sulphur, from various sources; and 50 per cent captan wettable powder (Orthocide), California Spray-Chemical Corporation, Richmond, Cal.

All plots received an annual dormant spray of bordeaux mixture to control peach leaf curl.

Mites were sampled, usually at two-week intervals, by collecting five to ten leaves from each tree except those in the outside rows of plots. At first, leaves within reach from the ground were collected at random but by 1953 many of the branches in the older orchards were beyond reach; in these orchards thenceforth three leaves within reach from the ground were collectd by hand and two from the top of the tree by means of clippers attached to a pole.

On the randomized single-tree plots, where more precise data were wanted, ten twigs were taken at roughly equidistant intervals about the tree. From each twig, two leaves were picked from short spurs at the base and four at equal distances along the terminal current season's growth. This method was devised to obtain more equal representation of leaves of different ages and positions, as determined by inspection of the growth habits of the trees in this orchard.

The leaves were held at about 40°F. in closed cans until the mites were to be counted; they remained in good condition for at least eight days if they were prevented from drying. During the earlier years the mites were counted under a stereoscopic microscope while still on the leaves but from 1952 the mites were brushed onto glass plates before being counted (Henderson and McBurnie, 1943). Direct examination of many samples of brushed leaves showed that an average of over 95 per cent of the motile stages of the mites had been removed.

The leaves from all trees in a plot were usually combined for examination but in some samples those from each tree were examined separately to determine the fiducial limits of the counts. When five leaves per tree were taken in a 31-tree plot with a mean of 8.7 European red mites per leaf the 95 per cent fiducial limits were 6.1 and 11.8; later in the season in the same plot the mean was 64.8 with limits of 43.9 and 85.7. In a 25-tree plot the mean was 260.3 with limits of 207.5 and 313.2. These limits, especially at the lower densities, were rather wide, but most samples included more trees and/or more leaves per tree and would be expected to have narrower limits.

The numbers of mites of the genus *Tetranychus* were much more difficult to determine accurately by random leaf samples because the infestations arise

near the trunks and seldom reach the outer part of the trees until the numbers are relatively large. Also, the colonial habits of these species cause great variation in numbers from leaf to leaf.

The brown mite spends much time on the bark of the twigs, especially when moulting and ovipositing. Studies carried out by the authors, to be published later, showed that the actual population on a peach tree can be generally estimated at two to three times as great as that estimated from leaf samples.

The peach silver mite is so small and sometimes so numerous that complete counts were impractical for most samples. The mites were usually counted on part of a single sector of the plate on which they were brushed. The numbers so obtained may not represent the actual numbers per leaf but they are comparable among plots and orchards.

A treatment was not continued on any one plot for more than three consecutive years for unavoidable reasons, usually because of outbreaks of scale insects that required treatment with parathion to prevent serious injury to the crop or trees. Experiments were also interrupted when the owners inadvertently sprayed plots with other materials.

European Red Mite

Effects of DDT.—The European red mite showed a general increase in Niagara district peach orchards during the decade previous to 1946, but injurious infestations were still confined to a few orchards and to certain years.

From 1946 to 1948, two annual applications of 50 per cent DDT wettable powder at two lb. per 100 gal. were made about six and three weeks before harvest to a plot in the Janzen orchard, in which all plots also received the usual four sprays of wettable sulphur each season. Fig. 1 (Janzen A) shows that the first year's treatment brought about an immediate and very great increase in mite numbers in the DDT plot as compared with the plot receiving sulphur only. The next year, however, the maximum count in the check was slightly above that in the DDT plot, the only occasion when this occurred. In 1948 the DDT plot continued to support a heavy infestation, whereas that in the check fell to a very low level.

After accidental spraying of the whole orchard with DDT in 1949, the positions of the DDT and check plots were reversed. Two applications in July of two lb. and one in late August of 1½ lb. of 50 per cent DDT wettable powder per 100 gal. were applied in 1950 to provide better control of the oriental fruit moth, *Grapholitha molesta* (Busck). In 1951 the DDT in the last spray was reduced to one lb. The experiment was interrupted in 1952 by an application of parathion to all plots to control scales, and was resumed with a different arrangement of plots in 1953 to 1955. Throughout these two periods mites consistently reached greater maximum numbers in the DDT plot (Fig. 1, Janzen B and Janzen C).

From 1949 to 1951 experiments were carried on in the High orchard, which had been uniformly sprayed with DDT by the owner in 1947 and 1948. A three-spray schedule similar to that in the Janzen orchard was followed, the last application containing two, 1½, and one lb. of 50 per cent DDT in 1949, 1950, and 1951 respectively. Three to four applications of sulphur were applied annually to all plots. In 1949 there was little difference in mite infestation between the DDT plot and the check, but the numbers of mites declined greatly in the check plot in 1950 and 1951 (Fig. 1, High).

In summary, the maximum seasonal densities of the mite populations in the DDT plots in both orchards were consistently high, whereas those in the checks

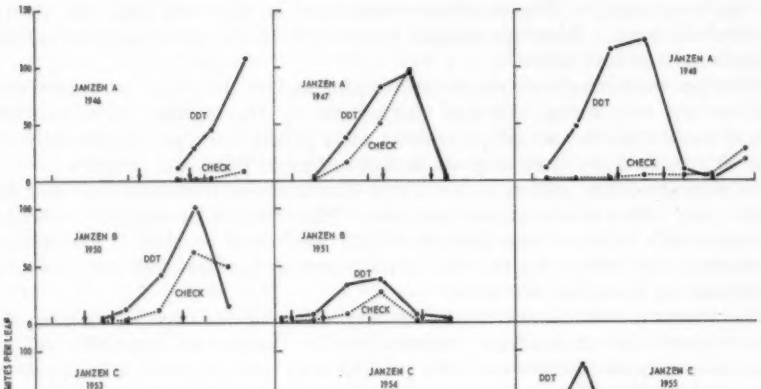

Fig. 1. Numbers of the European red mite per leaf in plots with and without DDT treatments in the Janzen and High orchards, Lincoln County, 1946-51. In the Janzen orchard, A, B, and C refer to different arrangements of plots. Arrows indicate spray dates. The last application in 1949 was at 1¼ lb. of 50 per cent DDT wettable powder per 100 gal.; in 1950 and later, 1 lb. All other applications were at 2 lb.

varied greatly, rarely equalling those in the treatments and usually being much lower. It will be shown later that sulphur, which was applied to all plots in both these orchards, may promote mite increase. Also, the checks were surrounded on at least three sides by DDT-sprayed orchards, which might have contributed to the numbers in the former by drift of mites or by obstructing the entrance of predators.

Fig. 1 shows that the maximum densities of mites in the DDT plots were generally lower from 1951 on than they were before. This was likely due to conditions peculiar to these orchards, such as competition from the two-spotted spider mite and possibly from honey dew-producing lecaniine scales, declining vigour of the trees with reduced leaf size, or other causes. It should not be construed as a general decline in mite numbers after prolonged use of DDT, for very heavy infestations persisted in other orchards. For example, in the Troup orchard, sprayed annually with DDT since 1947, acaricides were omitted from a plot in 1956 and 1957; as a consequence, in 1957 the European red mite rose to a very high maximum of approximately 140 per leaf.

The mites in some other orchards did not respond so quickly nor so strongly to DDT as they did in the Janzen, High, and Troup orchards. A plot in the Boothman orchard that was not treated with any pesticides in 1954 and 1955

received four annual sprays of DDT in 1956 and 1957, one at shuck-fall and two in July at two lb. and one about the middle of August at one lb. of 50 per cent powder per 100 gal. The initial density on June 19, 1956, was 0.05 mites per leaf; the maximum reached in the same year was only 14 and in 1957, 50. These results, and observations in other orchards, suggested that the rate of response to DDT depends to some extent on the initial density of the mites, that density presumably being regulated by previous spray treatment, tree nutrition, exposure to wind, or other obscure factors.

It had been noticed that very small blocks or single rows of peach trees sprayed with DDT within otherwise unsprayed orchards sometimes showed no obvious build-up of mites, suggesting that DDT exerted its effect only when fairly large blocks of trees were sprayed. To test this hypothesis, in 1957 an experiment was conducted on single trees in the Boothman orchard in a 48-tree plot that had received DDT in 1956 and was also uniformly sprayed three times with sulphur in 1957.

Ten trees taken at random through the plot were sprayed with two lb. of 50 per cent DDT on June 6, 26, and July 26. Ten other random trees were used as checks. Both sets of trees were sampled individually at weekly intervals. The average numbers of mites per leaf at fortnightly intervals were as follows:

	June 19	July 2	July 16	July 30	Aug. 13	Aug. 27
DDT	0.06	0.2	0.8	9.4	49.9	45.1
Check	0.05	0.05	0.1	1.1	10.4	24.2

By Student's *t* test, the difference between treated and check trees became significant at the one per cent level by July 16. The mite densities on these individual sprayed trees differed little from those in a companion plot sprayed throughout with DDT in 1956 and 1957, in which the numbers of mites reached 51 per leaf on August 13.

In 1958 a similar experiment was carried out in another block in the same orchard; in this case four sprays of DDT were applied, on June 19, July 3, July 22, and August 13. The average numbers of mites per leaf were:—

	June 24	July 8	July 21	Aug. 5	Aug. 19	Sept. 2
DDT	0.2	1.0	0.6	7.5	26.3	5.9
Check	0.2	0.2	0.2	1.7	4.2	2.6

The differences between treated and check trees were significant at the five per cent or lower levels on July 8 and subsequent dates. It is evident that DDT can bring about an increase of mites on single trees in an orchard; the apparent lack of increase in previous cases might have been more apparent than real, for visual estimates of an infestation are often misleading.

The seasonal development of a heavy DDT-promoted infestation of the European red mite on peach in general follows the usual trend of large populations reported by many authors (e.g., Chapman and Lienk, 1950; Cutright, 1951; Blair and Groves, 1952; Anderson and Morgan, 1958) on other hosts and arising from various causes: a very slow rise or even an apparent decline during the period of rapid foliage growth in June; a rapidly accelerating increase from late June or early July to a maximum in late July or, usually, in August; and a sudden crash to a small fraction of the maximum within one or two weeks. The decline was usually greater at higher maximum densities, so that plots with very heavy midseason infestations often had fewer mites in late August and September than plots with relatively small early infestations, which sometimes continued to increase until September. Typical examples are shown in Figs. 1 and 2. Owing to the rapid changes in density near the maximum, counts

made at two-week intervals sometimes failed to show the true peak of numbers; for example, the truncated shape of the curves in Janzen A, 1948, and B, 1951, probably indicates that the maxima were reached sometime between the dates of the highest two counts, for counts made at more frequent intervals in connection with other work showed that an infestation did not remain at a uniformly high level for any length of time.

On those few occasions when it was possible to continue sampling through September, the densities, after reaching a very low level, usually began to increase slowly and sometimes reached a value several times greater than that soon after the crash. This trend is shown in Fig. 1 (Janzen A, 1948; Janzen C, 1953 and 1955) and in Fig. 2. No explanation can be offered for this phenomenon, which has apparently not been reported before.

Effect of Parathion.—From 1949 to 1956 a plot in the High orchard received annually two sprays of 15 per cent parathion wettable powder at 1½ lb. in July and one at one lb. in late August, along with three to four sprays of sulphur. The maximum numbers of the European red mite per leaf each year from 1949 to 1955 were 0.7, 0.07, 2.0, 2.8, 4.0, 6.9, and 30.4 respectively. In 1955, a simple laboratory test was conducted to compare the susceptibility to parathion of the mites from this plot with those from the Janzen orchard that had received only one spray of parathion three years previously. Adult females were transferred to leaves on twigs in jars of water and allowed to ovipost for three days, when they were removed, the eggs counted, and the twigs dipped into suspensions containing 15 per cent parathion wettable powder at the rates of 0.75 or one gm. per l. Numbers of eggs per test ranged from 210 to 530. Living mites were counted seven days later, when all viable eggs had hatched. Among mites from the High orchard, 24 and 16 per cent of the possible numbers, based on egg numbers, survived the 0.75 and 1 gm. rates respectively, whereas none of those from the Janzen orchard survived at either rate. This test, although unreplicated, strongly suggested that the mites in the High Orchard had developed considerable resistance to parathion. Resistance in this orchard, and in the Niagara Peninsula in general, developed more slowly than in the Northwestern states where it appeared after three seasons' use of parathion (Newcomer, 1951, and other authors previously cited) and in parts of New York where it appeared after four seasons (Lienk *et al.*, 1952).

In 1956 the mites in the High orchard were not sampled often enough to determine the maximum numbers, but they were at least as great as in the previous year. In 1957 the owner resumed spraying operations but continued to follow a parathion schedule; the infestation continued to increase until, on August 14, 1958, it reached the remarkably high average of 260 mites per leaf. Many other heavily infested orchards seen in 1957 and 1958 indicated that parathion-resistant European red mites have become widespread.

The little experimental evidence so far obtained, supported by observations in owner-sprayed orchards, suggests that the continued use of parathion on resistant mites will result in annual infestations at least as heavy as those caused by DDT.

Effect of Fungicides.—Peach orchards must be sprayed several times during the season to protect the blossoms and fruit, especially near ripening, from infection by the brown rot fungus, *Monilinia fructicola* (Wint.) Honey. Until recently, sulphur was universally used for this purpose as no effective substitute was available until captan was introduced. Tests of the effects of fungicides on mite populations have therefore been practical only since 1953, and unsprayed

TABLE I.

Maximum numbers of the European red mite per leaf in peach plots in three orchards sprayed with fungicides only, Lincoln County, Ontario, 1952–56.

Fungicide	1952	1953	1954	1955	1956
Victoria orchard[1]					
Sulphur	20.1	4.8	7.8	–	–
Captan	1.5	2.4	7.7	–	–
None	1.7	1.6	6.0	–	–
Plant Pathology orchard					
Sulphur	–	4.8	1.0	8.3	2.4
Captan	–	4.6	0.7	2.2	0.5
Boothman orchard					
Sulphur	–	–	–	0.3	24.7
Captan	–	–	–	0.6	12.3
None	–	–	–	0.3	13.4

[1]Single plots; other orchards, averages of duplicate plots.

check plots could be used only in two small orchards at the Ontario Horticultural Experiment Station at Vineland Station, as the risk of excessive loss in commercial orchards was too great.

Timing of fungicide applications in all orchards was similar, namely, at the pink stage just before bloom, occasionally during bloom if the weather was wet, about shuck-fall, at the time of one of the oriental fruit moth sprays in July, and about August 25-28, three weeks before the expected date of harvest of the variety Elberta. In the Plant Pathology orchard another application was made just before harvest. Wettable sulphur was used at six to eight lb. and 50 per cent captan at two lb. per 100 gal.

In the Victoria orchard, single plots treated with sulphur or captan were compared with an unsprayed check. The Boothman orchard contained duplicate plots receiving sulphur, captan, or no fungicide, and the Plant Pathology orchard, duplicate plots receiving sulphur or captan. These three orchards were small and more or less isolated, and had histories of low mite infestation.

Except during 1955 in the Boothman orchard, the sulphur plots consistently supported the highest populations (Table I). The differences between the captan plots and the unsprayed ones were slight and inconsistent. The infestations never approached injurious proportions in any of the plots during the experiment.

From 1953 to 1955, sulphur and captan were compared in single plots in the Janzen orchard. Maximum numbers of the mites per leaf were as follows:

	1953	1954	1955
Captan	5	5	10
Sulphur	23	17	44

The foliage in the sulphur plot was badly injured by August each year, whereas that in the captan plot was still in good condition at the end of the season.

The same two fungicides were compared in duplicate plots in the Troup orchard in 1956 and 1957. The infestation in this orchard was high, possibly because of previous treatment with DDT, and all plots were badly injured in 1956; in 1957 the densities fell considerably. In both years the sulphur plots were the most heavily infested, as shown by the following average numbers of mites per leaf:

1956	July 9	July 30	Aug. 21		
Captan	3	20	64		
Sulphur	5	41	128		
1957	July 4	July 18	Aug. 2	Aug. 15	Aug. 28
Captan	1	1	5	30	31
Sulphur	2	2	32	75	34

On the whole, experiments with fungicides indicate that sulphur may promote increase in numbers of the European red mite but does not necessarily cause heavy infestations. The latter conclusion could, of course, be inferred from the status of the mite before 1946, when all Niagara peach orchards received sulphur but less than five per cent were seriously infested with the mite. Among the limited numbers of comparable captan-sprayed and unsprayed plots there was no indication that captan favoured increase of this mite as reported by Miller (1953) and Morgan *et al.* (1958).

Effect of Mite Infestations on the Orchards.—Although some of the experimental plots were infested with the European red mite for three or four successive years so heavily that the foliage was badly injured by mid-July, there was no obvious reduction in set of fruit, number or size of fruit at harvest, or general vigour of the trees as compared with adjacent plots in which acaricides had held the mites in control. Nevertheless, the loss of a large part of the food-elaborating cells of the leaves, equivalent to partial defoliation, must conceivably injure the trees in some way, and more precise measurement would probably reveal an effect on the crop, especially in trees growing in heavier, marginal soils. Part of the apparent tolerance of peach to mite attack may be due to the fact that mite-injured peach leaves, unlike those of apple and plum, do not fall prematurely in local orchards. Although Driggers (1946) reported that injury by the European red mite caused early leaf drop in New Jersey peach orchards, careful observations in adjacent plots with widely different infestations showed no sign of such an effect in the present experiments.

Tetranychus spp.

Two species of *Tetranychus* occur on peach in the Niagara Peninsula, namely, the two-spotted spider mite, *T. telarius* (L.), and the four-spotted spider mite, *T. canadensis* (McG.), usually in mixed infestations. Although *T. canadensis* was not recognized in the experimental orchards until 1954, it was undoubtedly present throughout the study, and has since been found to have a wider distribution in Niagara District orchards than *T. telarius*.

Before DDT was used, noticeable infestations of Niagara Peninsula peach orchards by either species were unknown, and infestations did not appear in the experimental orchards until several years after the first treatment with DDT. The maximum numbers per leaf in plots receiving three annual sprays of DDT, as well as sulphur sprays, in the Janzen and High orchards from 1949 to 1954 were as follows:

	1949	1950	1951	1952	1953	1954
Janzen	0.1	2.3	12.6	—	29.3	0.2
High	0.5	0.9	4.9	8.5	40.8	0.7

During this period the maximum density in any plot receiving sulphur only was six per leaf, in the Janzen orchard in 1953. The most abundant species in all plots during the heavy infestation of 1953 was *T. telarius*, as indicated by the orange-red colour of the diapause females in the fall; those of *T. canadensis* are pale yellow.

Density trends parallelling those in the experimental plots were observed

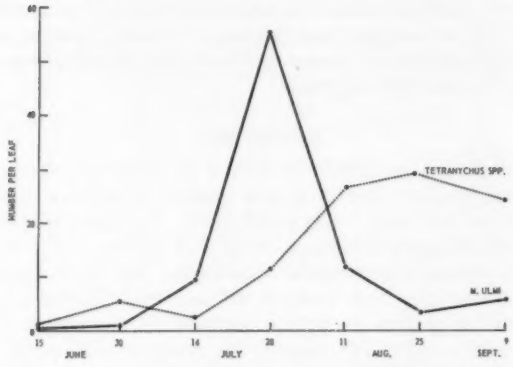

Fig. 2. Seasonal trends in numbers per leaf of the European red mite and of *Tetranychus* spp., mostly *telarius* (L.), in a DDT-sprayed plot in the Janzen orchard, 1953.

during the same period in a number of other orchards sprayed by the owners with DDT. The sudden decline in 1954 was due to some overriding factor, possibly weather, that affected the over-wintering population, operating throughout the district and independently of orchard treatment.

Infestations of both species since 1953 have generally been light, even in DDT-sprayed plots, although some build-up occurred in the Troup orchard, where maximum numbers per leaf in a plot receiving the standard three-spray schedule of DDT with captan as the fungicide and in a check plot receiving captan only were 12.2 and 2.1 respectively in 1956 and 14.3 and 0.2 in 1957. In this orchard *T. canadensis* was much more numerous than *T. telarius*. Both species were very scarce in the other fungicide trials.

Large numbers of *Tetranychus* spp. in the experimental plots and in other orchards have always been associated with considerably larger numbers of the European red mite. The seasonal development of heavy infestations of the two-spotted spider mite such as occurred in 1953 followed a different course from that of the European red mite, as shown in Fig. 2 for a DDT plot in the Janzen orchard; the two-spotted spider mite increased more slowly and reached its peak a month later than the European red mite and remained relatively abundant for a longer period. Chapman and Lienk (1950) and others also found that infestations of the two-spotted spider mite generally occurred later in the season than those of the European red mite in apple orchards. However, in many of these cases the course of the infestations of the two-spotted mite was complicated by late-season movement of the mites to the trees from the herbaceous vegetation of the ground cover. Such a movement did not take place in the experimental peach orchards, for these were cultivated to the end of June and the sparse cover of weeds that developed later bore fewer mites than the trees.

The moderate infestation of the four-spotted spider mite in the Troup orchard in 1957 closely parallelled the rapid build-up and sudden crash of the European red mite in the same plot. Too few infestations of either species of *Tetranychus* have been seen to determine whether they differ consistently in seasonal pattern.

It was noticed that the webbing spun over the under sides of the leaves by the two-spotted spider mite excluded the European red mite, and that the

former species was able to colonize leaves badly injured and abandoned by the latter. The nature of competition between the two species of *Tetranychus* and between these and the European red mite, and its effect on their respective populations, need further investigation.

Brown Mite

Morgan and Anderson (1957) described the form of the *Bryobia praetiosa* complex occurring on fruit trees as a new species, *B. arborea*, and suggested that it be called the brown mite. They (*in litt.*) also identified specimens from peach trees in the Niagara Peninsula as of this species.

Among the various experimental treatments, the most clear-cut effect on the brown mite was the high toxicity of sulphur. Frequently none of this species was found in several successive samples from sulphur plots whereas it occurred consistently, although usually in small numbers, in captan or unsprayed plots. For example, in the second year of similar treatment of the Troup orchard, a captan plot yielded 6.0, 4.5, 4.5, and 4.9 brown mites per 100 leaves from successive samples taken at two-week intervals from July 18, whereas none was found in two sulphur plots on either side of the captan one. Its susceptibility to sulphur was undoubtedly the reason why this species was virtually absent in commercial orchards until very recently.

Captan plots usually contained fewer brown mites than unsprayed plots. The plots were too few and the mite density was too low for this result to be conclusive and it may have been at least partly due to mechanical removal of the mites by the spray blast. It was at least evident that captan did not promote increase in the populations.

DDT plots without sulphur were available in only two orchards and for two seasons. In the first year of treatment (1956) of the Troup orchard, the members of the brown mite were negligible. In the second season the plot receiving the standard three-spray schedule of DDT plus captan had a maximum of 0.6 mites per leaf and one receiving only captan had 0.1 mites. In the Boothman orchard the plot receiving a three-spray schedule of DDT alone had maxima of 5.4 and 2.8 in 1956 and 1957 respectively; an unsprayed plot had 2.2 and 0.7 over the same period. These results suggest a positive but relatively mild response of brown mite populations to DDT. The DDT plots supported very large numbers of the European red mite, which may have affected the increase of the brown mite.

Although many Niagara district growers have followed a DDT-captan schedule for three or four years, no important infestations of the brown mite have been noticed. However, the acaricides usually added for the control of the European red mite may have also affected the other species. The behaviour of this species and its distribution on peach trees as determined from observations to be published elsewhere suggest that its populations on this host are self-limited at a relatively low level, and that it is unlikely to become a pest.

Peach Silver Mite

The peach silver mite has never been considered a pest of consequence in Niagara peach orchards. In some seasons young non-bearing orchards, which have not received sulphur sprays, may show some injury late in the season.

Another eriophyid, probably *Diptacus gigantorhynchus* (Nal.), whose usual host is plum, occurred rarely in some of the plots along with very much larger numbers of the peach silver mite.

Sulphur was very toxic to the peach silver mite (Table II), and captan

TABLE II.

Maximum numbers of the peach silver mite per leaf in peach plots in several orchards sprayed with fungicides only, Lincoln County, 1953–57.

Fungicide	1953	1954	1955	1956	1957
Victoria orchard					
Sulphur	3.5	0.7	–	–	–
Captan	48.8	6.9	–	–	–
None	51.5	129.0	–	–	–
Plant Pathology orchard[1]					
Sulphur	0.6	2.8	0.1	0.4	–
Captan	37.0	90.6	0.2	9.6	–
Boothman orchard					
Sulphur	–	1.1	1.3	–	0.3
Captan	–	42.4	33.6	–	–
None	–	89.5	517.9	–	599.4
Janzen orchard					
Sulphur	0.9	0.2	–	–	–
Captan	54.2	51.3	–	–	–
Troup orchard[1]					
Sulphur	–	–	–	–	0.9
Captan	–	–	–	–	19.2

[1]Averages of duplicate plots; other orchards, single plots.

sprays caused consistent and sometimes considerable reduction, possibly mechanically.

Few conclusions could be drawn as to the effect of DDT on the peach silver mite, owing to the very small number of trials in which DDT was used alone and to the erratic infestations of this species, but at least it had no obvious injurious effect.

It is doubtful whether the heaviest infestations of the peach silver mite that occurred during the study were really injurious. The mites were often not detected in the samples until after mid July and usually did not reach peak numbers before the middle of September or later. The lateness of attack should restrict its effect.

Conclusions

From the evidence obtained in the experimental orchards, it appears likely that if DDT and parathion were eliminated from the spray schedule, after a period of adjustment the population density of the European red mite in more than 95 per cent of the peach orchards of the Niagara Peninsula would remain below an injurious level as it did before 1946. If sulphur were replaced by captan the percentage would be still greater; the rare infestations that would arise might be ignored in view of the apparent tolerance of peach to mite injury. The two-spotted spider mite and the four-spotted spider mite would remain harmless even under a sulphur schedule if DDT were eliminated. The general use of captan in place of sulphur would undoubtedly lead to increased populations of the brown mite and the peach silver mite although the infestations would probably not be economically important. As long as pesticides like DDT and parathion are used the choice of fungicide is immaterial as far as control of mites is concerned.

Although the mite problem in Niagara peach orchards could thus be solved, such a prospect is not in sight. Modern fruit growing demands the

annual production of a crop with a high degree of freedom from insect injury. The sporadic attacks from the oriental fruit moth, with a large percentage of concealed injury in the fruit, are disastrous to orderly marketing and to establishment of consumer confidence, apart from the immediate loss to the grower. Fruit injury by the moth in the check plots in the Janzen orchard ranged up to 64 per cent and averaged 30 per cent over eight years. DDT and parathion give relatively cheap and effective control of the moth; some of the newer insecticides may prove to be equally or more effective but they are more expensive and all are broad-spectrum insecticides likely to have side-effects as undesirable as those of DDT or parathion. Ryania, which has been used so effectively as a selective insecticide against the codling moth in Nova Scotia (Pickett, Putman, and LeRoux, 1958), gave very poor control of the oriental fruit moth in tests by Mr. G. G. Dustan of the Vineland Station laboratory (unpublished). Only if another selective insecticide effective against the moth is discovered could DDT and parathion be omitted and the mite problem resolved.

Summary

In peach orchards of the Niagara Peninsula, DDT sprays promoted severe annual infestations of the European red mite, *Panonychus ulmi* (Koch), and more sporadic ones of the two-spotted spider mite, *Tetranychus telarius* (L.), and the four-spotted spider mite, *T. canadensis* (McG.). Numbers of the brown mite, *Bryobia arborea* Morgan & Anderson, were increased to a lesser extent. The European red mite developed strains resistant to parathion and became more troublesome than before this insecticide was used. Sulphur sprays generally promoted increases of the European red mite but these were not always serious. Sulphur was very toxic to the brown mite and the peach silver mite, *Vasates cornutus* (Banks). The fungicide captan showed no tendency to promote infestations of any species of mite.

Mites would evidently not be troublesome on peach in the area if DDT, parathion, and sulphur were omitted from the spray schedule, but omission of the first two materials is not practical because of the need of controlling the oriental fruit moth.

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Note on Occurrence of *Horogenes punctorius* (Roman) (Hymenoptera: Ichneumonidae), a Parasite of the European Corn Borer, *Ostrinia nubilalis* (Hbn.) (Lepidoptera: Pyralidae), in Southwestern Ontario[1]

By H. B. WRESSELL[2] and G. WISHART[3]

In a survey of infestation by the European corn borer, *Ostrinia nubilalis* (Hbn.), in Essex County, Ontario, in 1957, officers of the Chatham laboratory found several hymenopterous pupae associated with dead borers. Adults emerged in the laboratory and were identified by Mr. G. S. Walley, Entomology Division, Ottawa, as of *Horogenes punctorius* (Roman), an imported parasite of the borer. This is the first record of its establishment in Canada.

According to Baker *et al.* (1949), this insect attacks the corn borer in both Europe and the Orient. They also state that in North America it was first released in the Great Lakes area in Monroe County, Michigan, in 1926, and two years later in Lucas County, Ohio. From the Belleville laboratory more than 2000 adults were released in the Chatham district of southwestern Ontario and near the town of Essex in July, 1930, and in 1934, 215 were released at Dresden, Ontario. No recoveries were made by officers of the Belleville laboratory, although annual parasite surveys were made until 1949. Officers of the Chatham laboratory made annual surveys of infestation by the borer from 1946 onwards, but found no evidence of this parasite until 1957.

In 1957, four pupae of *H. punctorius* were found at three widely scattered places in Essex County and nine pupae were found during the infestation survey

[1]Contribution No. 3925, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.
[2]Entomology Laboratory, Chatham, Ontario.
[3]Entomology Laboratory, Belleville, Ontario.

in 1958. Of particular interest, however, was the high degree of parasitism of the borer in inbred corn grown for resistance studies at the Canada Experimental Farm at Harrow. Six plants in each of 31 single-row plots of corn were hand-infested in 1958 with 100 newly emerged larvae of the borer. These plants were dissected in early September to determine the borer population. The species of parasites and the numbers taken from the plots were: borer larvae, 483; *H. punctorius* 52; *Lydella* sp., 37; *Eulophus* sp., 8. Pupae and adults were also found in collections of the borer kept in cold storage for winter studies.

The sudden appearance of *H. punctorius* in Essex County is of interest from the point of view of insect dispersal. Baker *et al.* (*loc. cit.*) found that this parasite could maintain itself at a very low level after its initial release. Nevertheless, it seems unlikely that, had *H. punctorius* been present, no recoveries would be made in southwestern Ontario until 23 years after its final release in 1934. On the other hand, the possibility cannot be ignored that it entered Ontario from Ohio by way of the Lake Erie islands.

According to Rolston *et al.* (1958), the parasite *H. punctorius* remained at a low level in Ohio until 1951 but appeared to be well established in the western and northwestern parts of the state by 1955. He stated "However, it is perhaps indicative that in nine counties where collections were made in 1951 and 1955 (excluding Erie and Lucas) and where the parasite was recovered in either survey, the amount of parasitization increased in seven counties and the amount of parasitization more than doubled." This was confirmed by Mr. George T. York (in litt.), European Corn Borer Research, U.S. Department of Agriculture, Ankeny, Iowa, who informed us that the upward trend in Ohio was continued in 1956 and 1957. The state average for parasitization of the corn borer by *H. punctorius* was 11.5 per cent in 1957, and was the highest on record for Ohio. According to York (*loc. cit.*), *H. punctorius* is capable of travelling great distances. It has been recovered in Iowa 75 miles west of the nearest release point; this locality, in Sac County, was 150 miles west of the area where recoveries had been made in other years. It is therefore highly probable that *H. punctorius* arrived in Canada by flight from Ohio and is now well established in extreme southwestern Ontario.

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Food-Plant Distribution and Density and Larval Dispersal as Factors Affecting Insect Populations

By V. G. DETHIER
Zoological Laboratory, University of Pennsylvania,
Philadelphia 4, Pennsylvania

Introduction

It is generally agreed that insects whose larvae feed on plants do not increase to the larval food limit except in sporadic and unusual cases. In the few detailed studies which have been made, as, for example, Varley's (1947) study of the knapweed gallfly, the evidence suggests that the insects are held in check by parasites and predators. Andrewartha and Birch (1954) are of the opinion that shortage of food is probably the least important factor in limiting the numbers of animals in a natural population. On the other hand, they have pointed out (p. 489) that while it is unusual for an extensive population to consume all or most of the stock of food in its area, it does not follow that the amount of food is rarely of major importance in determining the numbers of a natural population. Several examples (p. 492) were given in which shortage of food was chiefly responsible for failure of population increase even though the absolute supply seemed adequate. In these cases local supplies were exhausted and the chance of finding fresh supplies depended upon the distribution and abundance of food and the powers of dispersal of the animals. In other words, the food was inaccessible relative to the animals' capacities for dispersal and searching.

It is obvious that the amount of food which can be utilized by phytophagous insects depends upon a complex variety of factors among which may be mentioned the size, number, and distribution of food-plants, the number and distribution of eggs laid by the insect, and the feeding and dispersal characteristics of the larvae. There are very few instances where these variables have been studied under natural conditions. The last mentioned factor, larval feeding and dispersal behavior, has rather consistently been neglected. As a consequence, it is not always known to what extent any one or combination of these factors limits the population.

With a view toward examining this problem, field studies of a butterfly, *Melitaea harrisii* Scud., were begun in East Bluehill, Maine. Although the studies have only been in progress for a period of four years, the data thus far obtained, together with an analysis of the land-clearing history of the area, have revealed some interesting relationships between food and population.

Feeding Habits and Dispersal of Larvae

M. harrisii is a small North American butterfly belonging to the family Nymphalidae. It lays its eggs in clutches of 20 to approximately 400 on leaves of *Aster umbellatus* Mill. which, in the area studied here, is the sole acceptable food-plant. The larvae are diurnal gregarious feeders. In the third instar they disperse, pass the winter in this stage, and complete their growth in the spring when they are solitary feeders.

Although an egg mass may be placed on any leaf of plants ranging in height from one to three feet, the larvae usually begin feeding at or near the top of the plant. They remain close together, frequently lined up side by side at the edge of the leaf upon which they are feeding, and spin a conspicuous nest in and on which they rest when not feeding. Gradually as leaves are consumed the colony works its way to the base of the plant. In no case during the period of study was it observed that the plant upon which the eggs were laid constituted a supply

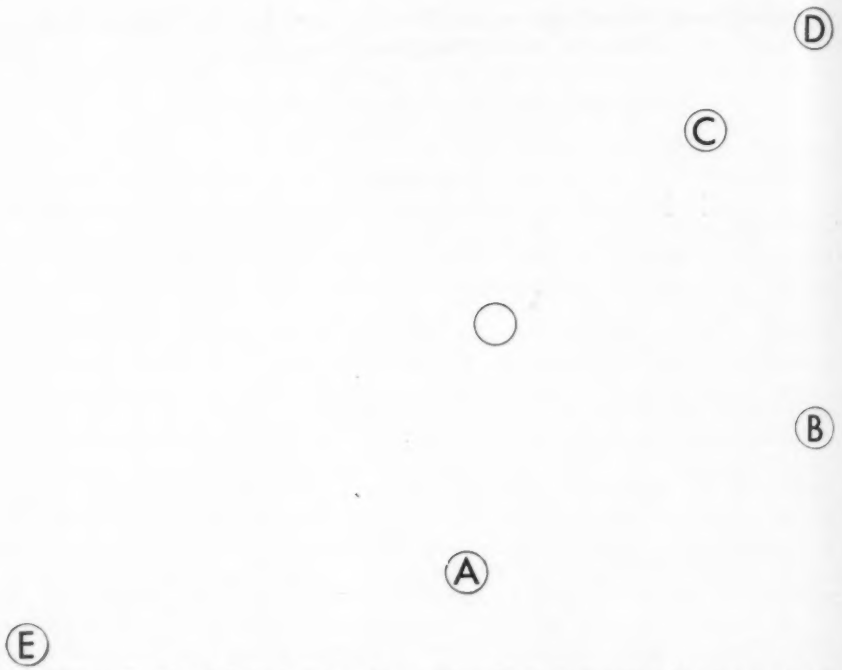

Fig. 1. Map showing the locations of aster plants A, B, C, and D with reference to the plant upon which 102 eggs had been laid. The distance from this plant to the next nearest plant (A) is 26 inches.

of food sufficient to meet the needs of the colony. Eventually larvae must migrate to other asters. Of course, when a small number of eggs is laid on a large plant, the larvae may grow quite large before being forced to migrate. Conversely, a large number of eggs on a small plant forces a migration when the larvae are still very small. The number of eggs laid on a plant bears no relation to the size of the plant. The time and number of migrations, therefore, is related to the number of eggs in a clutch and the size of the plant.

A superficial examination of a field in which *M. harrisii* colonies are feeding gives one the impression that the larvae unerringly locate new plants after having defoliated the first. Field experiments prove this impression to be false. Larvae can be made to emigrate by the simple expedient of removing all of the leaves from the plant upon which they are feeding. This procedure has been carried out with larvae of all ages.

Accounts of four experiments will suffice to explain what happens. In the first, involving a plant upon which 102 eggs had been laid, all leaves were stripped from the plant on the day that the eggs hatched. During the afternoon of the following day, the larvae began to migrate, and by morning all had departed. The next nearest plant was twenty-six inches distant. The locations of other plants are shown in Fig. 1. Two days later 11 larvae returned temporarily to the home plant. For the next ten days no larvae were found on any aster of the group. On the tenth day two larvae appeared on plant B (36 inches distant) and 18 on plant A (26 inches distant). No other larvae of this colony were ever recovered. Thus only 20, or about 20 per cent, of the original 102

Fig. 2. Map showing the distribution of larvae on aster plants 24 hours after all leaves had been stripped from the plant (28) upon which 400 eggs had been laid. The migrating larvae were in the first instar. The distance from 28 to 150 is eight inches.

larvae succeeded in reaching a fresh plant even though it was but 26 inches distant. As in the case of the species previously discussed, many larvae were lost to predators. Those which were not succumbed to starvation.

In a second experiment leaves were stripped from a plant bearing approximately 400 larvae. The next nearest plant was eight inches distant; the farthest, 49 inches. Migration began the same day. Twenty-four hours later the larvae were distributed as shown in Fig. 2. There were approximately 150 larvae on the plant eight inches away and 50 on the most distant plant. Three days later there was no change in distribution. Three hundred and fifty-nine, or 90 per cent, had successfully made the transfer. If the plant which was eight inches away is omitted from the calculations, 82 per cent of the larvae had found all but one plant within a three-foot radius.

In a third experiment a plant bearing 85 third-instar larvae was defoliated. The following day two larvae had departed. Four days later 21 remained on the home plant, 19 were on a plant seven inches distant, and the remainder had disappeared. Thus 19, or approximately 22 per cent, had made a successful transfer. The remainder never succeeded.

Experiment four consisted of depositing 157 larvae on the ground 12 inches away from an aster. Four hours later 81, or 52 per cent, had transferred successfully. At the end of twenty-four hours 64 per cent had transferred. There were no further additions.

Experiment five consisted of marking larvae from different clusters. Thirty larvae from each of four neighboring clusters were given distinctive marking. The relative locations of these clusters are indicated in Fig. 3. The home plants were then defoliated. Twenty-four hours later the marked larvae were redistributed as shown.

An additional marking experiment was made on two clusters of larvae which had emerged from two different clutches of eggs on neighboring plants (Fig. 4). Fifty larvae of one cluster were marked red, and 50 of the other, white.

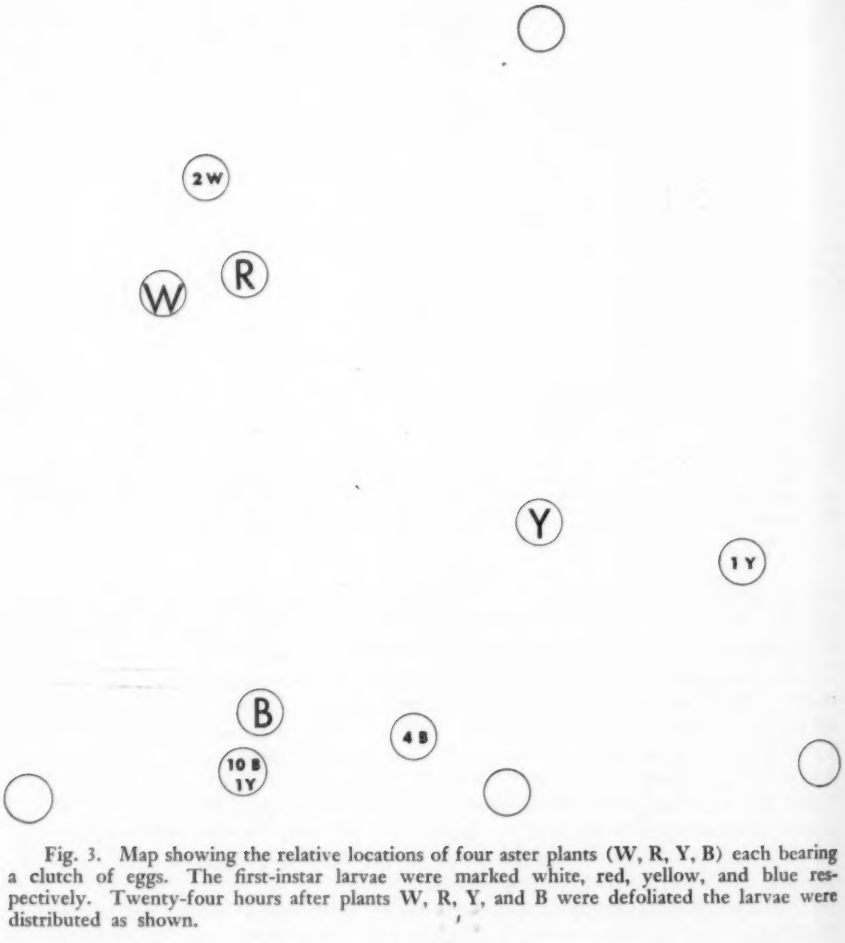

Fig. 3. Map showing the relative locations of four aster plants (W, R, Y, B) each bearing a clutch of eggs. The first-instar larvae were marked white, red, yellow, and blue respectively. Twenty-four hours after plants W, R, Y, and B were defoliated the larvae were distributed as shown.

The plants were then defoliated. Two hours later all of the white larvae and about half of the reds had deserted their respective plants.

Some of the whites were on red plants. Five hours later plant C had six whites and six reds, plant D, 17 whites and seven reds, plant E, 10 whites and 10 reds. Twenty-four hours later plant C had nine whites, six reds, and 13 unmarked; plant D had 22 whites, 22 reds, and 35 unmarked; plant E had 10 whites, 13 reds, and 27 unmarked. Plant B, the original red plant, had four reds still remaining. Plant A, the original white plant, had no larvae. At this time the total number of larvae in the group was 161. Two days later the number had decreased to 99.

Several conclusions may be drawn from these experiments. First, not all larvae succeed in finding new plants; second, success varies with the distance to be traveled and the stage of the larva; third, the necessity of migrating to find food greatly depletes the larval population by exposing its members to starvation and by prolonging the time during which they are at the mercy of predators;

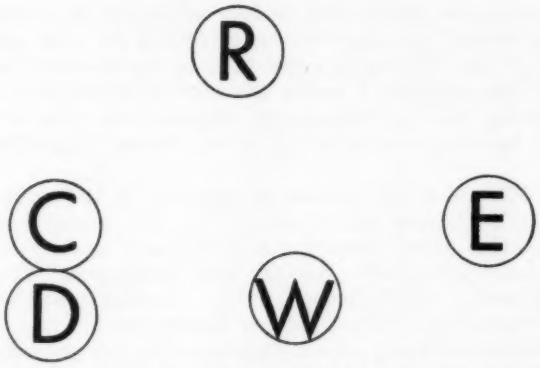

Fig. 4. Map showing the relative locations of five aster plants, two of which (R and W) bore a cluster of eggs. First instar larvae from the two clutches were marked red and white respectively and the plants defoliated. At the end of 24 hours the larvae were redistributed on plants C, D, and E as indicated in the text.

and fourth, there is apparently no specific colony coherence since larvae from different colonies mix.

Means Whereby Larvae Locate New Plants

Among the questions raised by these results is that of how the larvae locate new plants. Are there adaptations to insure success? The high losses attending migration suggest that chance plays a large part. When the larvae desert a plant, they give an appearance of randomness. Food being gone, the larvae become exceedingly restless and spend a great deal of time wandering over the defoliated plant. Then individuals crawl down the stem to the ground or to whatever vegetation touches the stem, or if encountering adjacent vegetation while crawling upwards, make the transfer. They may return immediately to the home plant or continue away. Larvae do not leave the plant in any fixed compass direction or sun direction. Being now in a jungle of vegetation, they progress through the jungle by walking along horizontal stems, making frequent intersections, and ascending and descending various plants. Individuals wander far alone, but the mass as a whole seems to push out and return and surge alternately. Although the larvae frequently spin fine silken threads, it does not appear that larvae of the species studied utilize these as trails as do certain other gregarious caterpillars (e.g. the tent caterpillar, *Malacosoma americanum* (Fabr.)) They appear to travel as individuals. The fact that they do not end up evenly distributed on all the plants in the immediate vicinity suggests the presence of some factor which biases dispersal. One possible suggestion is that specific orientating factors operate here.

All of the studies which have been conducted on the senses of caterpillars indicate that neither vision nor chemical senses can be effective in long-range orientation. Studies of form perception by Hundertmark (1937) and of the visual capacities of the ocellus by Dethier (1943) show that visual cues involving form can be expected to be operative over distances of the order of centimeters only. Under the field conditions experienced by *M. harrisii*, the stalk of an aster is just one more stem in a forest of stems; nor is it the largest or most conspicuous. There is no indication that the larvae can recognize the stem over distances greater than a few millimeters. Innumerable times larvae have been

observed approaching to within three or four millimeters of a stem only to turn away at the last moment, in some cases never to find the plant again.

Behaviour of this sort suggests that there is no olfactory cue effective at this distance. This suggestion is amply substantiated by the early work of Götz (1936) and Dethier (1937), subsequently confirmed by other investigators, to the effect that lepidopterous larvae do indeed possess a short-range olfactory sense.

A possible solution to the problem is suggested by the application of some of the findings of Wellington and his collaborators who, during recent years, have made extensive studies of the orientation of larval insects on the ground (Wellington, Sullivan, and Green, 1951; Sullivan and Wellington, 1953; Wellington, Sullivan and Henson, 1954; Wellington, 1955). It seems abundantly clear from these accounts that larvae do not wander at random but that they orientate with reference to the sun as a heat source and maintain any one orientation angle with respect to the sun by reference to the plane of polarization. This is best explained by quoting directly from Wellington (1955):

> "Until forward motion begins, there seems to be no good evidence that any factors are involved in the orientation but radiant heat from the sun, temperature as such, and the effects of wind upon temperature and upon the effectiveness of the thermal receptors. At the time travel begins, light has to be considered as a factor influencing *maintenance* of the orientation angle. The evidence points to maintenance of any one orientation angle by reference to a pattern derived from the plane of polarization of light from the overhead sky. As long as the *plane* remains *unchanged*, however, constant adjustments in course may be made to take into account temperature changes in the insect and its surroundings. In other words, although the overall temperature experience of the insect leads it to adopt one orientation angle with respect to the sun, and to maintain this angle during travel by reference to the plane of polarization, it is quite capable of adopting another angle and therefore of using a different polarization pattern as soon as its temperature experience stimulates it to do so. . . ."
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> "On the other hand, when the plane of polarization is not fixed, and major changes in it recur very quickly, the dependence of insects upon polarized light, instead of sunlight, is revealed. At such times, apparently disorientated movements . . . become common; and even the ability of an overheated insect to utilize radiant heat to guide it away from the direct rays of the sun is lost. In fact, it is common to see both larvae and adults fall victims of heat stroke on a sheet of paper while they are engaged in ineffectual circling movements in response to rapid changes in the sky. All insects observed seem quite incapable of completely discarding orientation by polarized light when the plane changes back and forth too rapidly for them to maintain a course by it."

When the terrain over which an insect is crawling is not uniform, further variables are introduced. As Wellington remarked;

> "Many natural surfaces are not at all uniform, but are broken, or creviced, or covered with pebbles or short vegetation. Consequently, they present a patchwork of physical factors such as surface temperature. Recognition of this is important if the movements of insects over natural surfaces are to be interpreted correctly. In addition, it should be clear that overheated insects need not turn away from the sun when they are on a broken surface or on short-stemmed vegetation. Many kinds of insects

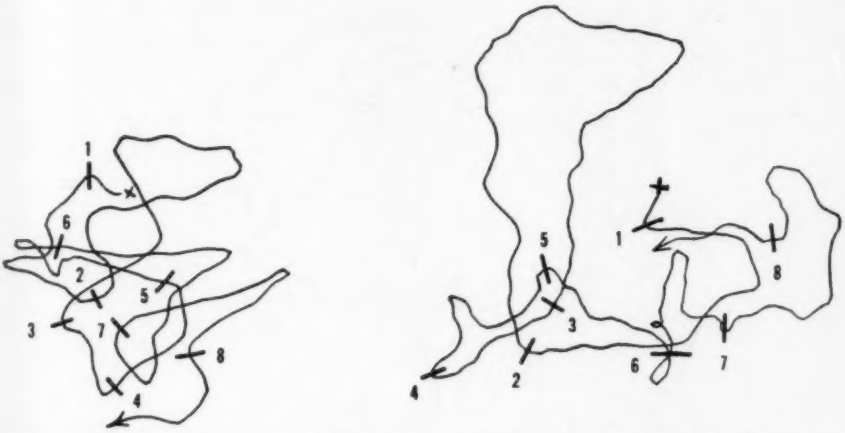

Fig. 5. Paths of two larvae of *M. harrisii* plotted simultaneously. Numbers refer to successive 10-second periods.

become negative to light as such when overheated, and those that do not still respond to gradients of temperature or moisture. Steep vertical gradients of all these variables often exist in rubble or low vegetation so that, often, overheated insects may move downward away from the sun, instead of turning away from it and continuing to travel over the surface."

The few experiments which have been performed with larvae of *M. harrisii* suggest very strongly that this species exhibits the patterns of behavior to be expected of larvae conforming to that described above. In the laboratory at 21°C. larvae were photopositive regardless of the nutritional state. In the field no such uniform orientation with respect to the sun was observed. On cloudless days the larvae usually followed straight paths with respect to the sun, sometimes toward it, sometimes away, and sometimes at a more or less fixed angle. Presumably these differences in direction were correlated with the temperature of the larvae, as Wellington has found to be the case in all species studied by him. Typical paths obtained on a three-foot square of white cardboard when experiments were carried out on sunny days with rapidly moving clouds are shown in Figs. 5 to 7. The paths are greatly convoluted and there is no consistent movement in any direction. As Wellington remarked in explaining similar paths which he had obtained with larvae of the tortricid (*Archips cerasivorana* (Fitch)), ". . . observation of a single insect would lead to the conclusion that it was completely disorientated, or that it was influenced by several stimuli at once."

From all of these considerations, it appears that once larvae have left their home plant the mechanisms of orientation which ensue are adaptations, not primarily for locating new food sources, but for insuring survival when the more immediate danger is death from overheating. This danger is illustrated in a case, admittedly extreme, in which migrating larvae of the red-headed pine sawfly were heat killed in large numbers (Benjamin, 1955). Thus, once larvae have departed from their home plant, their subsequent paths are random *insofar as other plants are concerned.* The finding of a new plant is a chance phenomenon. The larvae are moving out from a center not knowing where the nearest plant is and not being guided in any way toward it. The vagaries of temperature stimuli

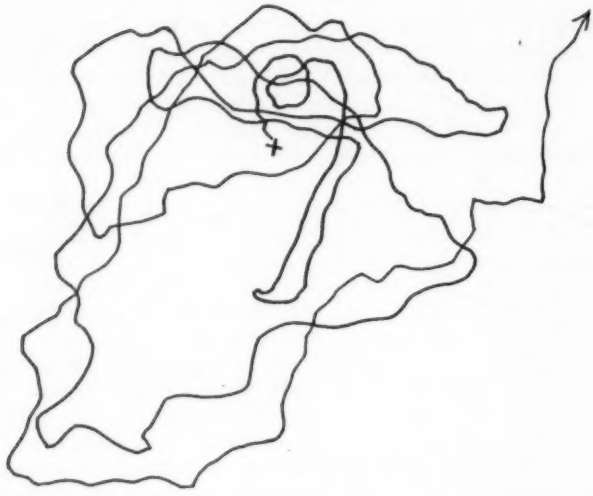

Fig. 6. Typical path of a larva of *M. harrisii* on a white cardboard in the field.

and clues from the plane of polarization make the movement essentially a random wandering. At the same time, such orientation as does occur might ensure that the bulk of the population is traveling *roughly* in the same direction; however, other individuals are traveling in different directions. The food-plants act as traps. If the larvae encounter a food-plant, they recognize it, cease their wandering, and ascend it. Having found a plant, the solitary larva or the one which is but loosely gregarious settles down to feeding after a preliminary period of exploration. A strictly gregarious larva like young *M. harrisii*, however, will not long remain on a plant of which it is the sole occupant. In sixteen different cases, starving individuals were placed on separate plants. Each fed briefly but eventually wandered away. To keep larvae of this species confined to a plant it was necessary to place at least two on the same plant. The value of this behavior is not clear. One possible advantage of gregariousness in early vulnerable stages is the added protection from parasites and predators which may be afforded by the extensive web-spinning. A single larva of this species is unable to spin sufficient silk to afford such protection.

Although one consequence of a female laying a very large number of eggs on a single food-plant is that the larvae are forced to migrate to secure adequate food for continued development, the provisions for finding food seem to be secondary to those for protecting the larvae from death by heat and for maintaining gregariousness. That as many larvae succeed in finding fresh food as do is principally due to the great density of aster plants.

Density of Larval and Food-Plant Populations

When counts are made of the numbers of food-plants in an area and the number of insects, it is surprising how much food is available and how little of it is eaten. A population of *M. harrisii* was studied in an isolated field (Fig. 9, Field C) which was completely surrounded by coniferous forest. This field has an area of approximately 43,200 square feet. In 1956 a census of adults showed only 24 butterflies. The sex ratio was not noted. These produced during that

Fig. 7. Typical path of a larva of *M. harrisii* on a white cardboard in the field.

summer 57 egg masses with an average of 200 eggs per mass. The field contained 9,462 aster plants. In 1957 there were 71 egg masses, also averaging 200 eggs per mass. A census of the adults who had laid these eggs was not taken. The aster count was approximately the same as the previous summer. Of the 14,200 larvae that these eggs produced, 34 were alive the following spring. Sample counts were made of the number of larvae per group in September just before they dispersed for hibernation. The number varied from four to 50, the average of 10 counts being 23.9. The number of larvae which retired for hibernation must have been on the order of 3,000. The following spring daily counts of mature larvae were made from the time asters produced leaves until the first adults appeared on the wing. The total number of larvae was 34. These gave rise that summer to 19 adults. During the summer (1958) 43 egg masses were produced. If the loss during the summer was the same as the previous year, only 21 per cent or 1,800 larvae entered hibernation.

Let us consider for a moment the situation as it existed in 1957. In the course of their development, the larvae from a single egg mass (taking into consideration the losses during dispersal) kill *at most* five plants. Thus, the 71 egg masses would in the normal course of events account for the loss of 355 aster

plants, or 3.8 per cent of the plant population. From these considerations it is clear that the field can support a much larger population of larvae than it actually does. There is a 79 per cent loss in larvae to predators and starvation during the summer. As the preceding section has indicated, this loss is due in no small measure to the added exposure imposed by the necessity of migrating from one plant to another. Thus by the time of hibernation the population has already been reduced to 21 per cent of the original. For the one year where figures are available hibernation imposed a further 99 per cent loss. In short, 14,200 eggs were required to produce an adult population of 19.

The History of *M. harrisii* in the Blue Hill Area

Although data on the early history, distribution, and abundance of *M. harrisii* are not available, the species not having been described until 1863, some knowledge of population trends and restraints may be inferred from facts which emerge from a combined study of the field habits of the species, the ecological history of a section of its range, and the present detailed local distribution and abundance.

Following the first recognition of the species it was collected over a wide area; however, its distribution was markedly discontinuous. It has always been known as a species which is "locally abundant" (Scudder, 1889). By 1889 it had been collected in Ontario, Quebec, New Brunswick, Nova Scotia, northern Wisconsin, Illinois, New York, and New England. At that time it was not known south of Massachusetts, but this must not be construed as meaning that it did not occur there. Its range is now known to extend south to Pennsylvania and West Virginia and west to Manitoba and Wisconsin.

The butterfly is restricted in its flying to open fields, meadows, and roads. In areas where fields are separated by forested areas the butterfly populations tend to remain more or less isolated because of the propensity of adults for open fields. The fields tend to act as traps keeping the adults within circumscribed areas. Where there are connecting roads, however, there is offered a means of communication with other fields. Adults have actually been observed using these roads. These are the same avenues along which the asters spread. Further evidence that the adults use roads is the fact that egg masses are commonly found on asters along roadsides in deep woods. Adults will range in open fields lacking asters but will return to roadsides for oviposition. Thus, larval populations are frequently concentrated along roadsides while flying adults will be concentrated in nearby fields even though these lack asters. As will be seen in the paragraphs that follow, the distribution and abundance of this species is closely tied to floral succession.

Prior to 1712 there were no Europeans in the Blue Hill area (Clough, 1953). According to the accounts of early settlers, the area was heavily and extensively forested. A few small salt marshes existed at some points along the coast, and there were as well, a small number of fresh meadows. Presumably asters grew here. Whether or not the Indians had cleared any areas for cultivation in this immediate vicinity prior to settlement by Europeans is not known with certainty. The area which was not forested was certainly negligible. Surrounding areas, as, for example, Long Island, had been subjected to clearing only shortly before this time, since lumbering began there as early as 1765 and shipbuilding as early as 1792. By 1824 a tremendous acreage of land had been cleared. Patches of woods, line trees, and occasional isolated trees were left standing.

Before 1800 the East Blue Hill area (three miles from Blue Hill) was under heavy forest. Settlement began about this time. In 1825 a road was cut through

along Morgan's Bay to the inland town of Ellsworth. A road was not cut through to Blue Hill until 1835. Extensive granite quarrying and metal mining began in this area in 1816. Shipbuilding and quarrying, the two industries which resulted in the greatest amount of clearing, continued until the 1890's.

The area was surveyed in the 1870's and '80's. An examination of a U.S. C. and G. S. map issued in 1885, discussions with several of the older inhabitants who were living in the area during the 1870's, and an examination of photographs made at that time revealed that lumbering, quarrying, and the requirements of living had resulted in clearing to the extent of providing almost continuous fields from Blue Hill to East Blue Hill.

Beginning probably with the "cold year" of 1816 when there was either ice or snow every month of the year (Day, 1954), farms were abandoned for better land in Ohio and the west. As the abandonment of farms continued following the Civil War, the end of mining interests, and the replacement of sailing vessels by steam and rail, fields were let lie fallow, and the forest began to return. At the present time, East Blue Hill-Blue Hill is essentially a forested area with scattered fields, pastures, and cut-over wood lots, connected in most instances by roads.

The history of this area is, then, one of nearly uninterrupted forest prior to 1750, extensive clearing for farming up to approximately 1820, maximum clearing by 1870-80 then gradual return of the forest and periodic rotational cutting for lumber until the present time. Some fields extant have been mowed annually since they were originally cleared. Thus, one is presented today with a picture of old permanent fields and those in various stages of succession.

Particular spots observed in the East Blue Hill area over the past ten years show that within two years of complete lumbering, asters have come in in maximum density. If the field is left untouched, raspberry, aspen, birch, bayberry, alder (if the land is low), laurel, and various other woody plants begin in five to seven years to crowd the asters. By 10 years from the time of clearing, the field is principally scrub with a thick but scattered growth of balsam, white pine, and spruce. In one particular field ten years after cutting, the conifers stood fifteen feet high. In the older wood lots which now separate the fields, the birches average 60 years, the balsams 35, the spruces 80, and the white pines 100 to 135.

It is reasonable to assume from the foregoing description that the aster population must have undergone a tremendous increase from 1750 to 1850. It is undoubtedly true that asters increased from the middle '70's to the '80's even though the plants may have been restricted to fence lines, hedgerows, and roadsides. With the abandonment of farms there must have been an enormous increase in aster population as mowing and tilling was suspended, followed by a decline as forests encroached. Some idea of the reduction in open areas may be gained by comparing Figs. 8 and 9, which represent a span of 73 years.

From the known behavior of *M. harrisii*, it is reasonable to suppose that maximum dispersal of the species probably occurred in the '70's and '80's, at the time of maximum clearing. With extensive continuous fields there would have been no barrier to the movement of the adults. As is the case today, adults probably laid their eggs far and wide along hedgerows, fence lines, and roadsides where asters would have escaped annual mowing. As the forests returned, contiguous open stretches existed no longer, and numerous fields became completely isolated or connected to the outside at best by a single road. This is pretty much the situation as it exists today.

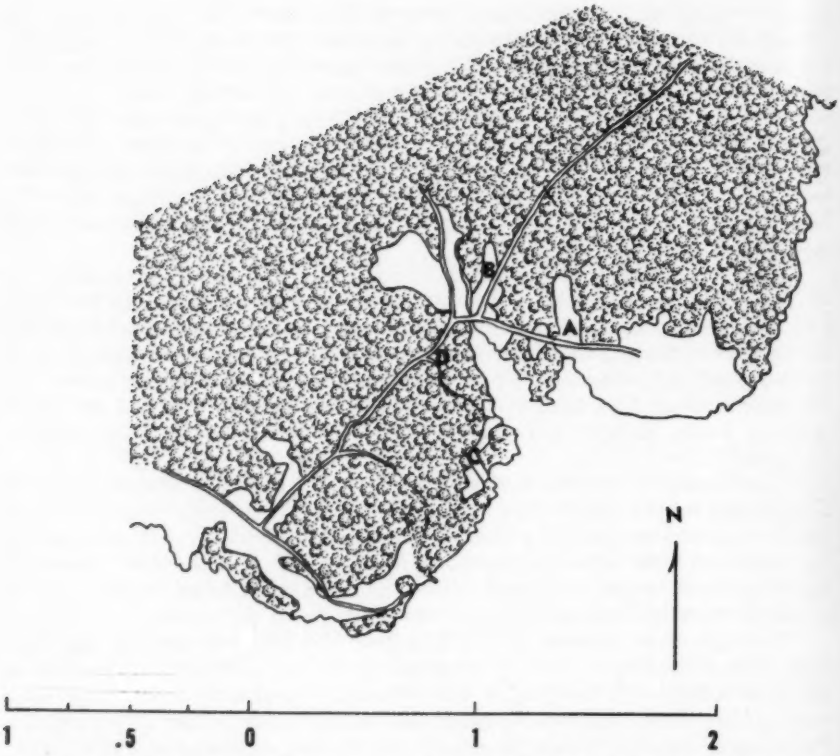

Fig. 8. Map of E. Bluehill, Maine, based upon U.S. C. & G. S. map issued in 1885 and showing the location of roads and clearings. The scale is in statute miles. A-D designate fields referred to in the text.

Certain happy circumstances of the behavior and ecology of *M. harrisii* present one with the unusual opportunity of making an extremely accurate total population (larvae) count of the species in an extremely wide area. As already described, the eggs are laid in batches on one particular species of aster. After the larvae hatch and commence feeding, they bind the leaves of the aster together against the stem in a web. The webbed leaves soon become brown, hence very conspicuous. If one is careful to choose as a time for counting that period after which all egg masses have hatched and before which larvae have begun to migrate, it is possible by inspecting all fields, clearings, and roadsides in the area under investigation to make a total count of larval groups. Setting the mean number of larvae per group as 200 (based on a count of 50 egg masses), a total larval census is possible. Such a census of the town of East Bluehill was made in 1958. The distribution and number of larval groups is shown in Fig. 9. There were in the area 21,200 larvae.

Several points of interest are revealed by this census: (1) the total population is small in terms of the size of the area (about seven square miles) and the number and extent of food-plants; (2) there is no relation between the number of larval groups in a field and either the area of the field or the number of asters in it;

Fig. 9. Map of Bluehill, Maine, based upon U. S. C. & G. S. aerial photographs. This represents the present distribution of forests and clearings. Letters designate fields referred to in the text. Numbers represent colonies of larvae.

(3) the distribution within the area is noticeably uneven, that is, the population is broken up into numerous small groups which are more or less isolated (and certainly would be were it not for connecting roads); (4) there is no obvious relation between the chronological age of a field and the density of larval population.

The final point may be elucidated further by a comparison of Figs. 8 and 9. Field A has been in existence 73 years. It contains asters but no larvae. It is possible that its isolation has been a barrier to adult immigration. Field B, in existence for the same period, is heavily populated. Field C, also of long standing, is heavily populated. Field D, a relatively new field, supported a small population. The figures do not show the distribution of asters since to ascertain this would have been a herculean task. It has been ascertained, however, that practically all of the roadsides in the area under consideration are bordered with asters as are also nearly all fields whether mowed annually or not. Fields which are not mowed are, of course, heavily populated throughout.

From the evidence presently available, it appears that in a given field the population of *M. harrisii* gradually builds up over a period of years. At the

same time succession gradually changes the nature of the field so that not only does the aster population begin to decrease, but the field becomes less a field and, accordingly, less suitable as a habitat for adults.

Discussion

Since the powers of dispersal of all small lepidopterous larvae are greatly limited, the success of a species with restricted larval feeding habits is influenced to a considerable extent by two factors: (1) the accuracy with which eggs are placed directly on or in close proximity to the proper food-plant; and (2) the total quantity of nutriment which the plant provides. It has been shown elsewhere that not all ovipositing females exhibit precision in the placement of eggs (Dethier, 1959). *Melitaea harrisii* is one species which has not been observed to err in this respect. It is, however, a species which typically lays a large number of eggs upon a single plant. As a consequence of this habit the larvae invariably defoliate the plant before development is completed.

There appears to be no relation whatsoever between the size of a plant (or the number of leaves thereon) and the number of eggs laid upon it. It might be argued that random oviposition possesses advantages insofar as protection against predators and parasites is concerned. If the greatest number of eggs were always placed on the largest plant, the predator could increase its efficiency by confining its search to the largest plants. As long as eggs are laid at random, search by predators would also have to be random. Therein lies an advantage to the prey.

On the other hand, the lack of correlation between the number of eggs and the size of the food-plant introduces the factor of starvation. When the plant constitutes an inadequate food supply for the total larval population (whether this be one larva on a minute seedling or 200 gregarious larvae on one aster), it frequently happens that the entire population is lost. The extent to which the population survives depends upon the dispersal powers of the larvae and the density of the food-plants.

When larvae have defoliated their food-plant, they begin to disperse. Although lack of food initiates dispersal, there is no indication that the wandering is food-directed. When orientation does occur, it appears to be, at least in part, an adaptation for protection against death by overheating. Larvae find new food-plants by chance alone.

There is no doubt in the case of *M. harrisii* that the number of food-plants growing in the area over which a population of adults range could support a much larger larval population than actually exists. The aster population is so dense and the larval population so small that a tremendous increase in the number of larvae would be necessary before any appreciable decrease in the aster population occurred. From this point of view, therefore, the total quantity of larval food is not a limiting factor.

On the other hand, the egg-laying habits of the species are such that food limits the rate of population increase. If, for example, the eggs which are laid on a single plant were distributed instead over a number of plants, a greater number of larvae of any given generation would attain maturity. Although the greatest mortality comes under the ambiguous heading of "winter kill," it might reasonably be assumed that this is not dependent upon the density of the population. Accordingly, if fewer larvae were lost by having to migrate from defoliated food-plants, the numbers surviving the winter would be greater. The small size of the population is, therefore, a consequence of the relation which exists between egg-laying habits, the abilities of larvae to disperse, and the density of food-plants.

Although these interactions keep the population at a lower level than an alternate set of actions would allow, there is no indication that they regulate the population in the sense of keeping it constant from year to year. Reasonably detailed information about *M. harrisii* points to large fluctuations in the local populations of this butterfly. The population is a slave to succession. When areas are cleared, the butterfly disperses more widely. This in itself does not cause an increase in population because the total number of eggs laid does not increase as a result of dispersion. However, extensive clearing also causes an increase in the aster population. If eggs laid by a far-ranging adult are placed where asters are very abundant, the dispersing larvae have a greater chance of finding fresh plants; hence, the number of larvae surviving will be greater. As the population of asters in a given field increases, the number of larvae which will complete their development increases, not because of the greater absolute supply of food which the increased aster population provides but because the increase in number of plants causes them to be closer together. The greater density of plants enhances their availability.

In short, it appears that local populations of *Melitaea harrisii* are not regulated in the sense of remaining at a constant density. Instead, the population increases as the density of food plants increases, and declines as succession reduces the density of plants. In this respect the rate at which the population increases and declines is markedly influenced by the availability of food.

Summary

The amount of food which can be utilized by phytophagous insects depends upon a complex variety of factors, among which may be mentioned the size, number, and distribution of food-plants, the number and distribution of eggs laid by the insect, and the feeding and dispersal characteristics of the larvae. A four-year field study of populations of the nymphalid butterfly *Melitaea harrisii* Scud. in East Bluehill, Maine, together with an analysis of the land-clearing history of the area has revealed some of the relationships which exist between food and population. Adults lay masses of 20 to 400 eggs on *Aster umbellatus* Mill. There is no relation between the size of the egg clutch and the size of the plant. In no case did a plant supply sufficient food for complete development of the larvae. Migration to fresh plants always occurred. Larvae never succeeded in reaching plants farther away than four feet. The mortality during migration may be as great as 80 per cent. Although lack of food initiates dispersal, there is no indication that wandering is food-directed. A census taken in one field indicated that the total adult population was 19 and that these had been derived from 14,200 eggs. A complete larval census made in an area of seven square miles gave a total of 21,200 individuals. Populations of *M. harrisii* fluctuate greatly. The population is a slave to succession and varies with changes in such human activities as lumbering, farming, etc. As the population of asters in a given field increases, the number of larvae which will complete their development increases not because of the greater absolute food supply but because plants grow closer together. In short, local populations are not regulated in the sense of remaining at a constant level. The rate at which the population increases and declines is markedly influenced by the availability of food.

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Studies of Predators of the Balsam Woolly Aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae) VI. *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae), an Introduced Predator in Eastern Canada[1, 2]

By N. R. Brown[3] and R. C. Clark[4]

Aphidecta obliterata (L.) is a common predator on conifer-infesting adelgids and aphids in Western Europe, including Scandinavia and the British Isles (Wylie, 1958b). The life cycle in Europe and descriptions of the various stages have been published (Weise, 1892; Portevin, 1931; Van Emden, 1949; Van Dinther, 1951; Wylie, 1958a). Beginning in 1941 several attempts have been made to introduce this species into Eastern Canada against the balsam woolly aphid, *Adelges piceae* (Ratz.). The initial liberations from England and Germany were apparently unsuccessful due to the inability of the insect to survive the Canadian winter conditions. Later collections were made in Sweden, Czechoslovakia, and Switzerland (Table I) from areas where the winter conditions more closely resemble those in Canada. These liberations also proved unsuccessful. The present paper brings together all available information on the liberations and related experiments obtained during the liberation years.

Liberations

Adults were released in areas of heavy *A. piceae* infestations, either in cages on infested trunks or as free releases at the bases of infested trees (see Clark

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[3]Professor of Forest Entomology, University of New Brunswick, Fredericton, N.B.
[4]Research Officer, Forest Biology Laboratory, Fredericton, N.B.

TABLE I.

A. obliterata liberations in New Brunswick and Newfoundland, 1941–1953

Locality	Origin in Europe	No. released	Year
NEW BRUNSWICK			
O'Dell Forest, Fredericton	England	1800	1941
Area 8, U.N.B. Forest, Fredericton	Germany	271	1951
Area 8, U.N.B. Forest, Fredericton	Europe*	2035	1952
Area 14, Wilsey Road, Fredericton	Switzerland	69	1955
Area 5, U.N.B. Forest, Fredericton	Sweden	222	1956
Area 18, Doak Road, Fredericton	Sweden	350	1957
3 locations, Fredericton	Sweden	601	1957
Oak Bay, Charlotte Co.	Switzerland	78	1955
Rexton, Westmorland Co.	Switzerland	67	1955
NEWFOUNDLAND			
John's Beach	Czechoslovakia	16	1957
Frenchman's Cove	Sweden	22	1958

*Germany, Switzerland, France.

and Brown, 1958 for description and photographs of cages). The majority of liberations were made in the vicinity of Fredericton at locations at least ¾ mile apart. Releases were also made in the southern part of New Brunswick and in the southwestern part of Newfoundland (Table I).

Establishment

Although this predator has been introduced into New Brunswick in six different years over the past 17 years and has been observed to complete a generation during the year of release, it has never been recovered in subsequent years. As the origin of the insects in Europe has ranged from continental areas to more maritime regions, and as they have been liberated in New Brunswick both inland and in coastal areas, it would appear that this species has been given every opportunity to become established and that it is incapable of surviving New Brunswick winter conditions. Also, no recoveries were made in Newfoundland in 1958 from the release of the previous year.

Life History and Habits

Adults have been released in the field in New Brunswick at the following times: 1941—April 26; 1951—August 8; 1952—June 19 to June 27; 1955—May 6 to May 27; 1956—June 4 to June 15; 1957—May 31 to June 6.

No recoveries were made following the 1941 release from England. In 1951, adults from Germany were held in cool storage at Belleville for slightly over one month and one-half were released at Fredericton in early August. The remainder were wintered in storage at Belleville for release in the early spring. The latter died during the winter and this is not surprising since the adults liberated in August were already sluggish and apparently unhealthy. When these were released some flew for distances up to 30 feet but most of them were observed to crawl up the trunk of the release tree to a maximum height of 10 feet. One pair was observed *in copula* for 25 minutes. One adult was seen on August 9; subsequent to this none were observed. Of 100 adults caged on August 8, 59 were still living on September 11. These were transferred to an over-wintering cage built of wire screening in the form of a cone around the base of a tree. No adults emerged from hibernation to the base of this tree in the spring of 1952.

In 1952, adults from Germany, Switzerland, and France were released between June 19 and 27. They were observed in small numbers as late as August 19 but none were subsequently seen and they were not recovered in the spring of 1953.

Wylie (1958b) states that in the Vosges Mountains of Europe there is one generation of *A. obliterata* each year and that emergence of the new adults begins in mid June. It is to be supposed that the adults released in New Brunswick in 1952 were adults that had just emerged and so would not oviposit until the following spring. This is supported by the fact that no eggs were observed in either of these years, even when the adults were caged. The adults released in 1955, 1956, and 1957 were received earlier in the summer and were probably individuals that had overwintered and were ready to oviposit.

In 1955, all 69 adults from Switzerland were released in a sleeve cage as they were received (May 6 to 27). On June 14 the cage was removed and the adults still living were allowed to disperse. Eggs were first seen on the bark under the cage on May 16 and on June 24, 56 eggs in small scattered groups were observed on the trunk. First-instar larvae were first noted on June 24 and a few were present up to July 5. After this no stages were seen on the release trees. One pupa was found on a nearby tree on July 13 from which an adult emerged in the laboratory on July 18.

In 1956, adults from Sweden were released both in the open and in cages from June 4 to 15. Adults were observed to July 3, and many small groups of eggs were noted on the release trees from June 13 to 24, with counts as high as 90 eggs being made. Larvae were first seen on June 29 although some eggs had probably hatched a few days previous to this date. Last-instar larvae were last seen on July 18, and pupae were present on July 18. Adults from these pupae were not seen and the species was not found in the release area in the following year.

Releases were made in 1957 at several locations near Fredericton and in Newfoundland. Those released near Fredericton were from Sweden; those in Newfoundland from Czechoslovakia. As in previous years adults were observed for a short time following release and eggs and a few larvae were present on one tree.

In 1958, 22 adults from Sweden were released in Newfoundland. No recoveries have been made.

It is not possible to describe a natural seasonal history for this insect in Canada. Wylie (1958b) describes the life cycle in the Vosges Mountains of Europe as beginning with adult female appearance in April, oviposition from about mid April to mid June, larval activity from late April to June, pupation beginning in early June and adults first emerging in mid June. Total developmental time was 38 to 41 days.

According to Smith (1958), *A. obliterata* adults will feed on all stages of *A. piceae* except the settled neosistens. Smith also reports that all larval instars eat eggs and adults of the prey, the third- and fourth-instar larvae being capable of consuming from 200 to 350 eggs in each instar. Prey eggs, crawlers, intermediate stages and adults were present in the field at Fredericton when released adults and their larval progeny were feeding and these stages were all eaten.

Wylie (1958b) noted cannibalism in laboratory rearings. We have observed newly-hatched larvae in the laboratory and in field cages feeding on one another as well as on unhatched eggs. We have not seen larvae feeding on other predacious larvae nor being fed upon by them, although Wylie stated that both occur under experimental conditions and in the field in Europe.

Control Value

Since the predator has not become established at Fredericton, control value is not known. An example of its potential control value has, however, been witnessed. In 1952, large numbers of adults (up to 525) were released on individual heavily-infested trees. During the week following, reduction of intermediate stages and adults of the prey *A. piceae* ranged from 52 to 92 per cent. A similar reduction did not occur on other infested trees adjacent to these and the reduction is attributed directly to predation by the adult beetles released on the trees. Apparently the adults fed actively following liberation and, after eliminating a large part of the prey population, left the release trees and scattered throughout the surrounding forest in search of additional food.

Summary

1. *Aphidecta obliterata* adults have been released at Fredericton on six occasions, and at two other locations in New Brunswick. Releases have been made in Newfoundland in two successive years.
2. When the adults were liberated early in the summer a complete generation has been observed in the field during the year of release.
3. Recoveries have not been made in any locality in the year following release, even when adults had been observed late in the previous summer, prior to hibernation.
4. The reason advanced for the lack of establishment is the inability of the adults to survive winter conditions in central New Brunswick.
5. Observations by Smith (1958) and Wylie (1958b) on feeding habits of larvae and adults have been corroborated.
6. Since the species did not become established it was impossible to obtain information on control value except for that resulting from extensive feeding by adults immediately following release in large numbers on individual heavily-infested trees.

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Book Review

Manual of Insect Morphology by E. Melville DuPorte. Reinhold Publishing Corporation, New York. 224 pages. Price $5.00.

Dr. DuPorte's manual for the laboratory study of insect morphology fills a need that has been felt by instructors in entomology for a number of years. It has grown from the much-revised laboratory outline that the author has used in conjunction with his lectures at Macdonald College. The book is admirably arranged; a gradual progression from simple concepts and dissections to more complex ones is made from chapter to chapter. Thus at the same time that the student's knowledge of his subject is increasing his skill in making successively more complex dissections is developing to the point at which he may profitably undertake the more delicate internal dissections outlined in the latter portion of the book.

Thirteen chapters are devoted to external morphology. Successive chapters deal with metamerism, the structure of the abdomen, thorax, abdominal and thoracic appendages, male and female genitalia and the head and its appendages. A full chapter is devoted to the physical and chemical properties of the body wall and its histology. Six chapters covering the alimentary, respiratory, circulatory, reproductive and nervous systems and the sense organs complete the section devoted to internal morphology.

Individual chapters discuss first the more generalized, then the more specialized conditions of anatomical structure and the dissections outlined are based on insects representing many orders. For the most part, the study material suggested is easily obtainable in the field or from a biological supply house. The manual is adaptable to morphology courses of varying lengths and comprehensiveness. By selecting examples for dissection from the large number outlined by Dr. DuPorte, the instructor can readily tailor a laboratory course to his requirements.

For insect morphology courses of more limited scope Dr. DuPorte's book could well serve as text as well as laboratory manual. His introductory paragraphs in each chapter outline the generalized form of any structure or group of structures and their orientation. The possible phylogenetic development of specialized structures is discussed and in many cases the comparative morphological and embryological evidence to support these conclusions is presented. More controversial subjects, such as the nature of the metamerism of the insect head, are discussed in greater detail and various viewpoints are presented.

It is unfortunate that a glossary of morphological terms has not been included in the manual to assist the student in the laboratory. This is especially true when one considers that the index it not comprehensive and perhaps not even complete. Neither "legs" nor "thorax" are included in the index for example, although "wings" and "head" are. These, however, are only minor criticisms of an outstanding contribution to entomological literature. Perhaps the greatest compliment that one can pay to Dr. DuPorte on the publication of his book is to say that his text is as lucid as the lectures which he has delivered to more than a generation of entomologists.

DAVID F. HARDWICK

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